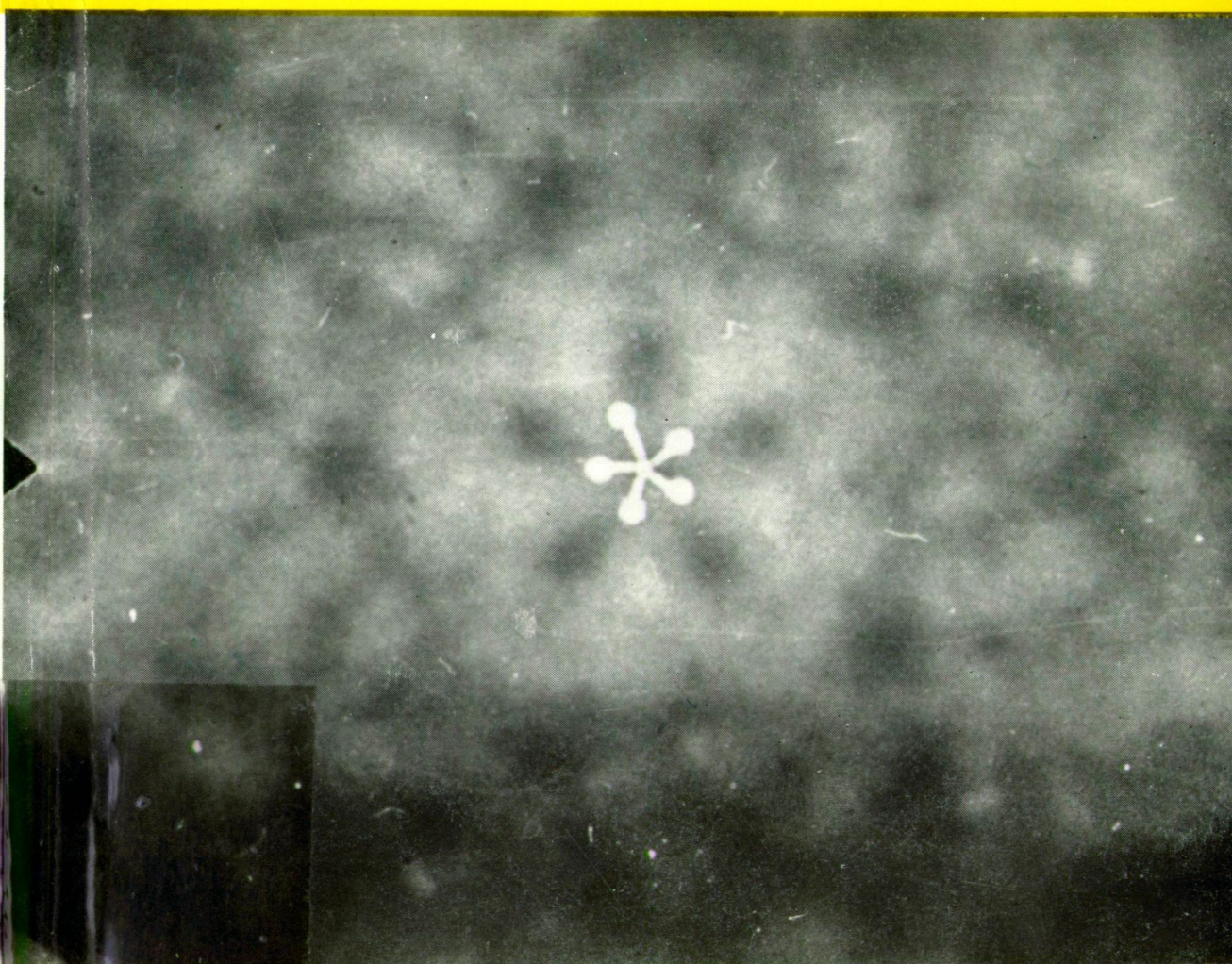
PLANT CELL BIOLOGY AND DEVELOPMENT

EDITED BY

M. KEDVES



Plant Cell Biology and Development

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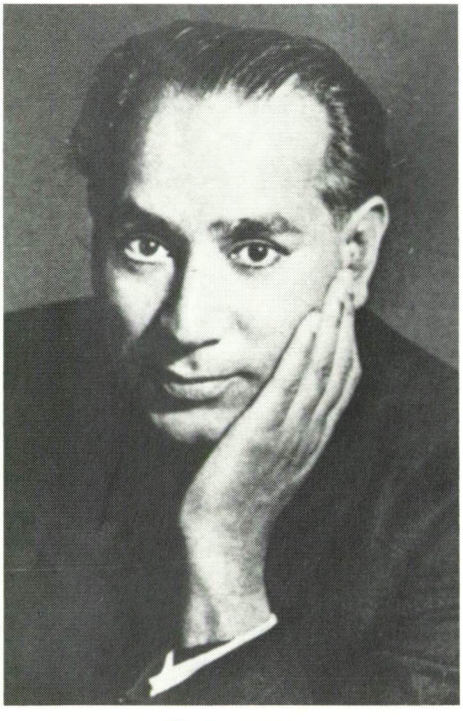
Preface

This number is dedicated to the Birbal Sahni Centenary



Photograph 1

Dr. BIRBAL SAHNI professor, 1891—1949

Photograph 2

Madam SAVITRI SAHNI, 1902—1985

Photograph 1 was reproduced from the Birbal Sahni Memorial Volume (The Palaeobotanist, vol 1), photograph 2 from the commemorate paper of Dr. (Mrs) CHHAYA SHARMA, Grana *24*, p. 137. Reproductions and enlargements were made by Dr. I. BAGI and E. FARKAS.

It was a long time ago when I as student and later as a young assistant to Professor P. GREGUSS in the Department of Botany of the University of Szeged, that I learned and started the investigation of the anatomy of the secondary wood of

recent and fossil species. During these studies I got acquainted with the outstanding standard work of the Birbal Sahni Institut. Scientific contacts were well established between the two institutions not only through the common interest in the investigations of secondary wood anatomy, but also when the palynological investigations on the Hungarian Tertiary sediments were started in Szeged, by Dr. J. MAÁCZ, Dr. P. SIMONCSICS and myself. Personal contacts with Dr. B. V. VENKATACHALA, Dr. S. C. SRIVASTAVA, and Dr. M. B. BANDE strenghtened the contacts. It was a great honour for me that the Birbal-Savitri Sahni Foundation asked me to deliver a lecture at the Savitri-Sahni Smarak Lecture series.

Now on the occasion of the Birbal Sahni Centennarium my laboratory will express our respect to the great scientist but at the same time not forgot his wife, Mrs SAVITRI SAHNI who was his helpmate during his lifetime. I think that to draw the character of the scientific aims and concepts of Professor SAHNI some citations from the Birbal Sahni Memorial Volume are the best illustration.

SAHNI M. R., p. 6: "BIRBAL's interest were wide and, if I might say so, Lamarckian in scope. To this his discovery of the coin moulds at Rohtak in March 1936 bears witness. This archaeological discovery by a palaeobotanist, with the stroke of a geologist's hammer, symbolizes the vitality and versatility of the man. It is a tribute to his genius that not only did he make this unique discovery, but also threw himself heart and soul into the study of these coin moulds."

P. 8: "BIRBAL was always a dreamer and a visionary."

"Towards this end he worked incessantly, enriching his collections of fossil plants by field work and exchange and by building up the finest library for palaeobotanical work in India."

RAO, A. R., p. 10: "As in teaching, so in research he emphasized hard and careful work, accuracy and attention to details.

'Hard work killed no body'

was a frequent saying of his. He liked intensive work on any problem more than extensive work."

P. 11: "He himself had a worldwide correspondence and exchange of reprints and his collection was easily one of the best in the East.

P. 14. "One of Prof. SAHNI's most often quoted papers of theoretical interest is the one 'On the ontogeny of vascular plants and the theory of recapitulation'. In this paper he pointed out several examples amongst vascular cryptogams, gymnosperm seeds and angiosperm flowers, to show that the well-know biological principle."

MAHESHWARI, P., p. 17: "SAHNI's first paper entitled 'Foreign Pollen in the Ovules of *Ginkgo* and of Fossil Plants' was published in the New Phytologist of 1915, only a few years after he reached Cambridge. Here he recorded the presence of pollen grains other than those of *Ginkgo* in no less than eight out of about a dozen ovules of this plant obtained from Montpellier. Most of them showed the presence of two prothallial cells thus indicating their abietineous nature and one had germinated to form a tube twice as long as its own diameter." P. 18: "Soon after the publication of his papers on *Nephrolepis,* SAHNI submitted a dissertation for the SUDBURY-HARDYMAN PRIZE on the 'Evolution of Branching in the *Filicales*' which was published in the New Phytologist of 1917". "In the year 1920 SAHNI published another paper dealing with seed structure of *Taxus* and suggested that the Palaeozoic seeds

Cycadinocarpus, Rhabdospermum, Mitrospermum and *Taxospermum,* all belonging to the *Cordaitales,* illustrated the general tendency which may have operated in producing the types of seeds found in *Taxus, Torreya* and *Cephalotaxus*." P. 19: In 1924 Prof. SAHNI, then Head of the Department of Botany at the Lucknow University, was elected President of the Indian Botanical Society which had been founded only three years earlier as the result of his own efforts and those of Profs. W. DUDGEON (Allahabad), S. R. KASHYAP (Lahore) and K. RANGACHARI (Madras), none of whom is with us any more. The subject of Prof. SAHNI's presidential address was 'The Ontogeny of Vascular Plants and the Theory of Recapitulation'."
HALLE, p. 22: "Even a cursory glance at BIRBAL SAHNI's work on fossil plants inevitably conveys a vivid impression of its extraordinary compass and variety. His researches, in fact, ranged over practically the whole field of palaeobotany."
Following S. R. NARAYANA RAO, p. 48: "No notice of Prof. SAHNI's work or life would be complete without a reference to his wife, SRIMATI SAVITRI SAHNI, whose understanding sympathy and companionship meant everything to him. She always accompanied him on his scientific travels and took part in many of his geological excursions. Her unfliching devotion in no small measure contributed to the great scientific achievements of Prof. SAHNI.

Finally, I would like to point out as follows:

The inter- and multidisciplinary research concept was not only emphasized by Professor SAHNI, but was realized, too, in his work. I would like to stress again and again the importance of the hard work as a single way for scientific advancement.

The necessity of a world-wide correspondence and publication exchange, which seems to be now also the unique opportunity to keep the world standard in the scientific research activity.

The life and the work of Prof. SAHNI is an excellent ideal for the young students and young scientists.

Szeged, 8. April, 1991.

M. KEDVES
head of the laboratory

1. PALAEOBOTANICAL INVESTIGATIONS ON PLANT IMPRESSIONS AND SPOROMORPHS FROM EGYPT

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Abstract

Impressions of fragments of vegetative and reproductive organs of a few members of *Bennettitales* including a new species of male organs; *Williamsonia aegyptiaca* sp. nov. and two new foliage species; *Otozamites major* sp. nov. and *O. daragii* sp. nov., as well as impressions of fragmentary remains of conifers are recorded from presumably Lower Cretaceous beds in the western side of Gulf of Suez. All fossils except *O. major* are recorded for the first time from Egypt. Three samples containing plant macro-remnants were investigated palynologically. Lower Cretaceous spore-pollen assemblages were found.

Key words: Palaeobotany, macro- and micro-remnants, Lower Cretaceous, Egypt.

Introduction

The location of Abu-Darag area and a brief description of its geology were previously given in a preliminary paper by EL-SAADAWI and FARAG (1972). Their paper included also drawings of two vertical sections of the two kaolin quarries D and H of the locality. These two sections showed the sequence of different kinds of strata in the two quarries. They also showed the presence of plant remains in only three beds; namely beds g and w of section H and bed v of section D. A brief description of the construction and thickness of the three fossiliferous beds, as well as, a description of the principal fossils (*Otozamites* sp. and cf. *Phlebopteris*) were given.

Material and Methods

The first author (W. EL-SAADAWI) visited the locality several times, and his collection (kept at the Botany Department, Faculty of Science, Ain Shams University), now includes over 200 specimens coming from the three beds as follows:

172 Slabs from bed g of section H,
5 Slabs from bed w of section H,
8 Slabs from bed v of section D,
23 Loose specimens.

The flora of bed g consists of fragmentary remains of bennettites, ferns a few conifers and some other unidentifiable plant remains. All are preserved as impressions with no organic matter left. The fossil plants of bed v of section D are also in the form of impressions but there is always a thin carbonaceous film left. In this bed neither bennettites nor conifers were found, only ferns or fern-like foliage in addition to some insect remains. The five slabs of bed w; which most probably represents a natural extension of bed v, and the 23 loose slabs have not yet been examined. The description of the fossil flora of Abu-Darag is proposed to be in a series of papers; I-*Bennettitales* and *Coniferales*, II-*Filicales* and other unidentifiable plant remains of bed g, III-The flora of beds w and v and the associated insect remains, IV-The succession of plant remains in the three fossiliferous beds and the bearings of the floras as a whole on the geology of the area and the age of the strata which is presumed to be Lower Cretaceous (ABDALLAH et al., 1963).

For the investigation of the plant microfossil remnants the samples were treated first with HCl. After washing with water HF was added to the organic matter containing residue to eliminate the silicates and other inorganic components. Finally, the slides for light-microscope investigations were prepared in glycerin-jelly.

Results

PLANT MICROFOSSILS

I—A. *BENNETTITALES*

The remains of this group of plants represent dominant components of the flora of bed g. The vegetative organs are abundant whereas the fructifications are rare. Thus out of the 172 slabs of bed g: 74 slabs contain fragments of one type of leaf, 22 slabs contain fragments of a second type of leaf, and 7 contain fragments of male organs.

The male reproductive organs are assigned to the genus *Williamsonia*. The leaf types are assigned to the genus *Otozamites*. Fronds of the latter genus are know to be borne on trunks and branches of the former.

DESCRIPTION OF THE FOSSILS

CYCADOPSIDA

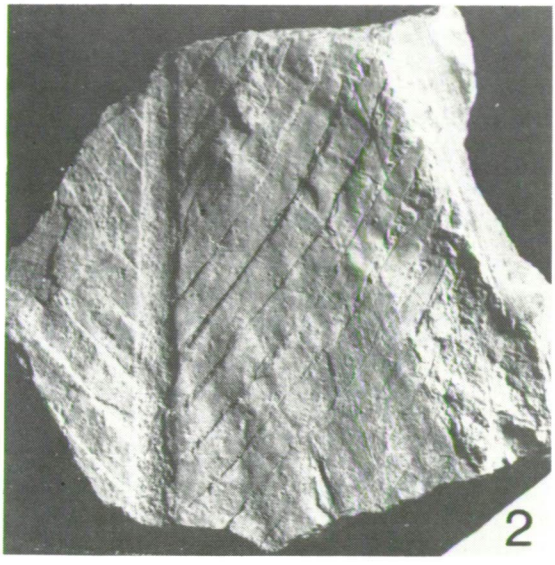
BENNETTITALES

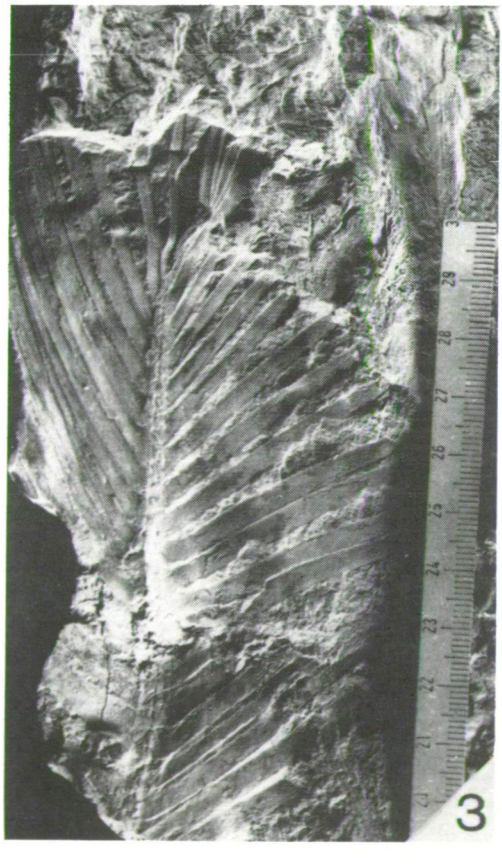
WILLIAMSONIACEAE

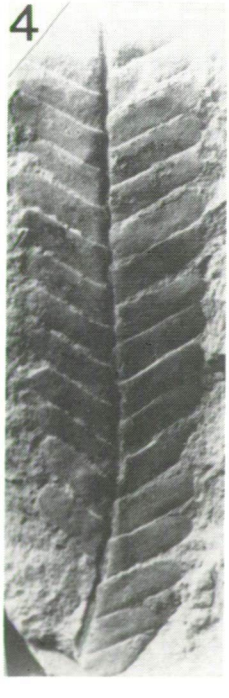
Otozamites Braun.

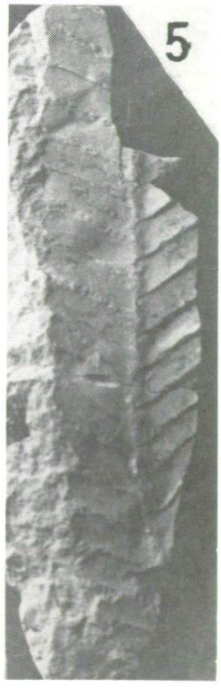
Otozamites major sp. nov.
(Plate 1.1., fig. 1—3, plate 1.3., fig. 8, text-fig. 1.1., 1.2.)

Remark. — Although this species is represented in a large number of slabs (74) yet unfortunately its remains are fragmentary and the shape of the leaf as a whole remains unknown. Nevertheless, the following description and establishment of a new species is based on the study of this large number of specimens.









◀ Plate 1.1.

1. *Otozamites major* sp. nov. Impressions of a fragment showing adaxial surface and pinnae bases. Specimen H 73. Magnification 0.75 x.
2. *Otozamites major* sp. nov. Counter part, showing abaxial surface. Specimen H 73. Magnification 0.75 x.
3. *Otozamites major* sp. nov. Impression showing leaf apex (an impression of a *Pinus* stem is seen in the right upper corner of the figure). Specimen H 54. Magnification 0.76 x.
4. *Otozamites daragii* sp. nov. Impression of the lower half of a frond showing abaxial surface. Specimen H 30. Magnification 1.14 x.
5. *Otozamites daragii* sp. nov. Counter part of the same specimen showing pinnae bases. Specimen H 30. Magnification 0.92 x.

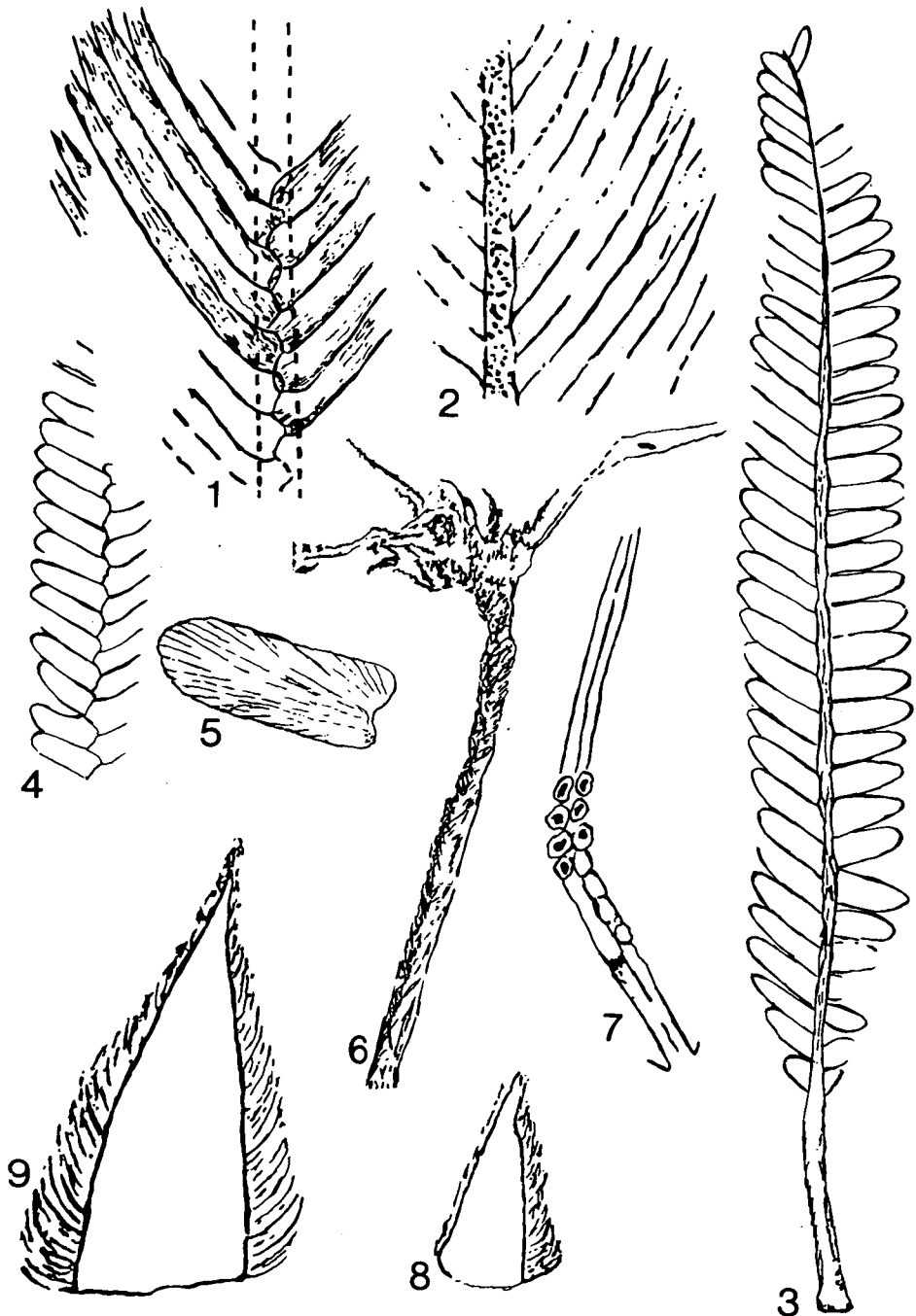
Diagnosis and description

The largest specimen is a leaf fragment about 20 cm long. The lower end of its rachis is 9 mm wide and there is a gradual decrease in width towards leaf apex. Complete small pinnae are 3.5—5 cm long and 3.5 to 6 mm broad. Larger pinnae; 9 mm wide were found. These large pinnae were incomplete at their upper ends, however, their length may be estimated at 15 cm. The pinna tapers very gradually towards its apex. The latter is rounded and not sharply pointed. The pinnae may be straight, slightly or somewhat strongly curved (Plate 1.3., fig. 8). The angle of insertion of the pinnae on the rachis is generally between 45° and 55°. The pinnae are closely set together but sometimes there is a narrow gap; usually under 2 mm in between. The pinnae cover the upper surface of the rachis completely so that the auricles generally overlap and the lower margin of each pinna overlaps the upper margin of the pinna below (text-fig. 1.1.). The lower surface of the rachis is finely ornamented (text-fig. 1.2.). The preservation of some pinnae was good enough to show some 18 veins that are slightly divergent at the rounded base of the pinna but are paralell upwards. It is not clear whether these veins were devided or not. Both margins of the pinna are incurved at the base. The latter is asymmetric with an acroscopic auricle (text-fig. 1.1.). The pinnae are flat with entire margins. The material of the lamina is not thick and the veins are somewhat more prominent on the lower than on the upper surface.
Comment. — This species of *Otozamites* being present in a large number of slabs is therefore, closely associated with almost all other fossil plants present in bed g.

Otozamites daragii sp. nov. (Plate 1.1., fig. 4, 5, plate 1.2., fig. 6, 7, text-fig. 1.3—1.5.)

Diagnosis and description

This species also has a once pinnate frond but is much smaller than the previous species. Many fragments were met with in 22 slabs. An almost complete frond is shown in text-fig. 1.—3., and Plate 1.2., fig. 6, 7. The leaf has an elongated lanceolate shape and is 2.5—3 cm broad. Its full length might have been 25 cm. The pinnae are generally 12 mm long and 3.7 mm wide. Extreme length and width are 18 mm and 4.5 mm respectively. Smaller pinnae were recorded. The pinna is



Text-figs. 1.1.—1.9.

1.1, 1.2. *Otozamites major* sp. nov.
1.3—1.5. *Otozamites daragii* sp. nov.
1.6., 1.7. *Williamsonia aegyptiaca* sp. nov.
1.8., 1.9. Hairy-bracts (*Williamsonia* sp.)

straight; the two margins of the lamina run parallel throughout most of the length of the pinna and the apex is broadly rounded (text-fig. 1.3.—1.5.). The auricle is scarcely developed in some of the pinnae and undetected in others, but there are usually auricular veins (text-fig. 1.5.). The lower margin of the lamina is clearly incurved at the base in some pinnae. In other pinnae it was difficult to determine whether it is incurved or decurrent. Veins are divergent, branched, and about 14 of them traverse the lamina at its centre. The angle of insertion of the pinnae on the rachis is generally about 60°. The specimen shown in text-fig. 3 (see also Plate 1.2., fig. 6, 7) has one row of pinnae with the usual angle of insertion (60°). While the other row has a wider angle of about 80°. Such difference in the angle of insertion of the two rows of pinnae of a leaf is sometimes seen in pinnate leaves of some extant plants. What is interesting to note is that in the present specimen the pinnae of the row with a wide angle are evidently shorter and broader than those of the opposite row. This is possibly due to the slope of the rachis during the life of the plant. The pinnae are closely set and possibly overlap at the base. The ornamentation pattern of the lower surface of the rachis is different from that of the previous larger species. The pinnae are flat with entire unspecialized margins. The material of the lamina is thin.

Comment. — Similar to the previous species this one is also closely associated with almost all other plant remains present in the bed.

Williamsonia CARRUTHERS

Williamsonia aegyptiaca sp. nov. (Plate 1.3., fig. 9, text-fig. 1.6., 1.7.)

Remark. — Fragments of male organs, especially the pedicels were met with in 7 slabs, usually in close association with *Otozamites daragii.* Line drawing of the best specimen (Plate 1.3., fig. 9) is shown in text-fig. 1.6. It is mainly upon this specimen that the following description and establishment of a new species *Williamsonia aegyptiaca* is based.

Diagnosis and description

This male flower has a long pedicel of a uniform breadth of about 1 cm throughout the portion preserved which is over 20 cm long. All recorded pedicels were of about the same breadth ranging between 10 and 12 mm. Pedicels must have been thick since they are preserved as moulds. The specimen shown in text-fig. 1.6. represents almost half the male organ with about 8 microsporophylls which are united at their base in the form of a cup.

The microsporophyll after becoming free from the basal cup moves obliquely upwards and outwards for a length of about 5 cm then it bends and stretches more horizontally for six more centimeters. This however, does not represent the entire length and shape of the microsporophyll since the distal end is not preserved. However, the entire length of the microsporophyll may be estimated at 14 cm. The diameter of the basal cup is about 3.5 or 4 cm. Therefore, the diameter of the fully expanded "flower" might have been 25—30 cm. The adaxial surface of the

6

7

◀ Plate 1.2.

6. *Otozamites daragii* sp. nov. Impression of the major part of a frond showing lower surface. Specimen H 30. Magnification 1.14 x.
7. *Otozamites daragii* sp. nov. Counter part of a portion of the same in addition to the basal part of the leaf. Specimen H 30. Magnification 1.25 x.

sporophyll (see text-fig. 1.7.) has two rows of depressions; one row on each side of a median ridge. Each row consists of about 8 of these depressions which are supposed to represent the positions of the synangia. No remains of the latter were found. The microsporophyll is 6 mm wide at its middle part and 3.5 mm at its broken end.

Hairy-bracts (*Williamsonia* sp.) (Plate 1.3., fig. 10, text-fig. 1.8., 1.9.)

Six relatively large hairy bracts (most probably of *W. aegyptiaca*) were met with in six specimens. They were usually found in association with *Otozamites major*. They are broad with remarkably long marginal hairs which are curved upwards (Plate 1.3., fig. 10, text-fig. 1.8., 1.9.). The bracts vary in size to some extent and the largest bract (text-fig. 1.9.) measures about 50 mm in length and 1.5 cm (2.8 cm including the hairs) in breadth.

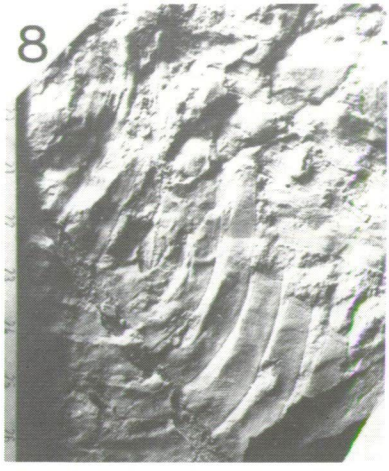
?Female "flowers" (of *Williamsonia aegyptiaca)* (Plate 1.3., fig. 11, 12)

Two specimens comparable to casts and moulds of the basal portion of *Williamsonia gigas* ovulate strobili (see later under comparisons) are shown on Plate 1.3., fig. 11, 12. The specimen shown in fig. 12 represents a mould of the basal portion of an ?ovulate cone. The maximum diameter of the portion preserved and illustrated is 16 mm. The rays or sterile organs surrounding the central, circular depression are about 3.5 mm long by 1 mm broad, and their number is about thirty. The second specimen (Plate 1.3., fig. 11) represents a cast of the basal portion of an ?ovulate cone about 5 cm in diameter. The position of the pedicel is shown as a hollow space surrounded by a number of basal scales.

Identification

Comparing *Williamsonia aegyptiaca* and the two species of *Otozamites* described in this work with all forms of the two genera described and illustrated in the available literature showed that they could not be accomodated in any of them. Naturally they approach some of them more closely than others but they remain distinct from them all. Since the comparison included a relatively large number of species, therefore, it was plausible to establish the three new species.

Otozamites daragii sp. nov. is so close to the boundary between *Otozamites, Ptilophyllum* and *Zamites*. But according to the definition of Harris (1949a) it should be included in the genus *Otozamites* for the characteristic type of the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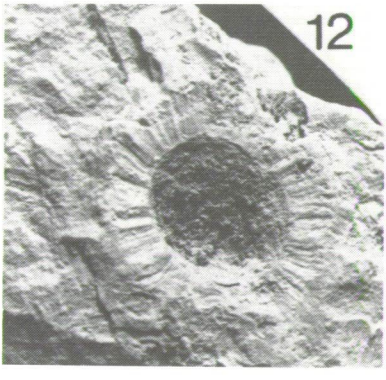
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10

◀ Plate 1.3.

8. *Otozamites major* sp. nov. Fragment showing curved pinnae. Specimen H 5. Magnification 0.7 x.
9. *Williamsonia aegyptiaca* sp. nov. Impression showing long pedicel and about 7 microsporophylls. Specimen H 24. Magnification 0.64 x.
10. *Williamsonia* sp. Hairy bract, showing long marginal hairs. Specimen H 26. Magnification 1.8 x.
11. *Williamsonia* sp. Cast of an ?ovulata cone. Specimen H 14. Magnification 1.25 x.
12. *Williamsonia* sp. Mould of an ?ovulate cone. Specimen H (Hb) 33. Magnification ca 2 x.

venation of pinna base, if not for the presence of an acroscopic auricle and an incurved basiscopic margin in some of the pinnae.

The hairy bracts and the ?ovulate cones do not offer sufficient information regarding their structure and organic connection to allow for more precise determination than rather assigning them to the genus *Williamsonia.*

Comparisons

The two new species of *Otozamites* of Abu-Darag were compared with more than 20, mainly Jurassic, forms of that leaf genus, e.g. with those illustrated and described by Arnold (1947), Edwards (1929a,b), Harris (1944, 1949a,b), Mägdefrau (1956), Sahni and Rao (1933), Seward (1911, 1917), Sporne (1965), Thomas (1913), Tralau (1968) and Wieland (1916). The comparison showed clearly that the two species of *Otozamites* of Abu-Darag could not be accomodated in any species of the genus. However, *Otozamites daragii* has some features in common with *O. feistmanteli* Zingo which is described and illustrated by Harris (1949a), but it is more closely similar to *O. reglei* var. illustrated and described by Wieland (1916) from the Jurassic of Oaxaca Mexico. Wieland's (1916) figure 70 of *Otozamites reglei* var. is very similar to the line drawing of *O. daragii* shown in text-fig. 1.3. of the present work. However, there is a slight difference in the angle of insertion of the pinnae on the rachis. Those of *O. reglei* var. have slightly wider angle.

Williamsonia aegyptiaca agrees with *W. whitbyensis, W. spectabilis,* Wieland (1916), and *W. santalensis,* Sitholey and Bose (1953) (=*Weltrichia,* Bose 1967), all of Jurassic age, more or less in the size of the basal cup. The new species agrees with *W. whitbyensis* in the manner in which the fertile organs (synangia) are arranged on the adaxial surface of the microsporophyll, but differs in this respect from all other male "flowers", e.g. *W. mexicana, W. spectabilis, W. santalensis.*

W. aegyptiaca differs from other species in the length of the microsporophyll; that of the new species being the longest. The microsporophyll also differs from others in its general shape and curvature. The diameter of the fully expanded "flower" of *W. aegyptiaca* is almost larger than that of all other flowers. The one nearest to it is *W. santalensis (=Weltrichia).* The pedicel of the new species is long and thick with no paralell in the other species. The latter are reconstructed without a pedicel or with a short slender one.

The hairy bracts of Abu-Darag are broader than any such organs described in literature, e.g. Harris (1953) and Wieland (1916). In length they are as others. The hairy bracts of *Williamsonia harrisiana* (female flower) described by Bose (1968)

from the Jurassic of India have prominent marginal hairs that are very similar to those of Abu Darag's specimens.

The mould here, referred to as an ?ovulate cone resembles to a certain extent the "mould of basal portion of an ovulate cone of *Williamsonia gigas*" illustrated and described from the Jurassic of Yorkshire by WIELAND (1906). Abu Darag's ?ovulate cone mould shows also slight superficial resemblance to *Sturiella;* a bisexual "flower" referred to the *Williamsoniaceae,* ANDREWS (1961). Abu Darag's ?ovulate cone cast resembles to a certain degree the "Strobili casts of *Williamsonia gigas*" illustrated and described from the Jurassic of Yorkshire by WIELAND (1906, 1916). It also resembles the "cast of the ovulate-cone base of *Williamsonia netzahualcoyot*" described and illustrated in association with *Otozamites reglei* from the Jurassic of Mexico by WIELAND (1916).

I-B *CONIFERALES*

The flora of bed g is dominated by cycadophyte and fern remains whereas the conifers are quite rare. The following are the fossil conifer impressions discovered:

- Two stem-fragments of *Pinus.*
- One fragment of an *?Araucaria* twig.
- A fragment of a ?leaf.
- A single cone specimen (part and counter part).
- A single fragment of a ?cone (part and counter part).
- A single fragment of a stem with a ?cone base attached.
- Nine seeds (or ovuliferous scales).

DESCRIPTION OF THE FOSSILS

In view of the small amount and conditions of preservation of the fossil material of the discovered conifers, only brief descriptions and comparisons of the fossils are given, however, accompanied with instructive illustrations.

CONIFEROPSIDA

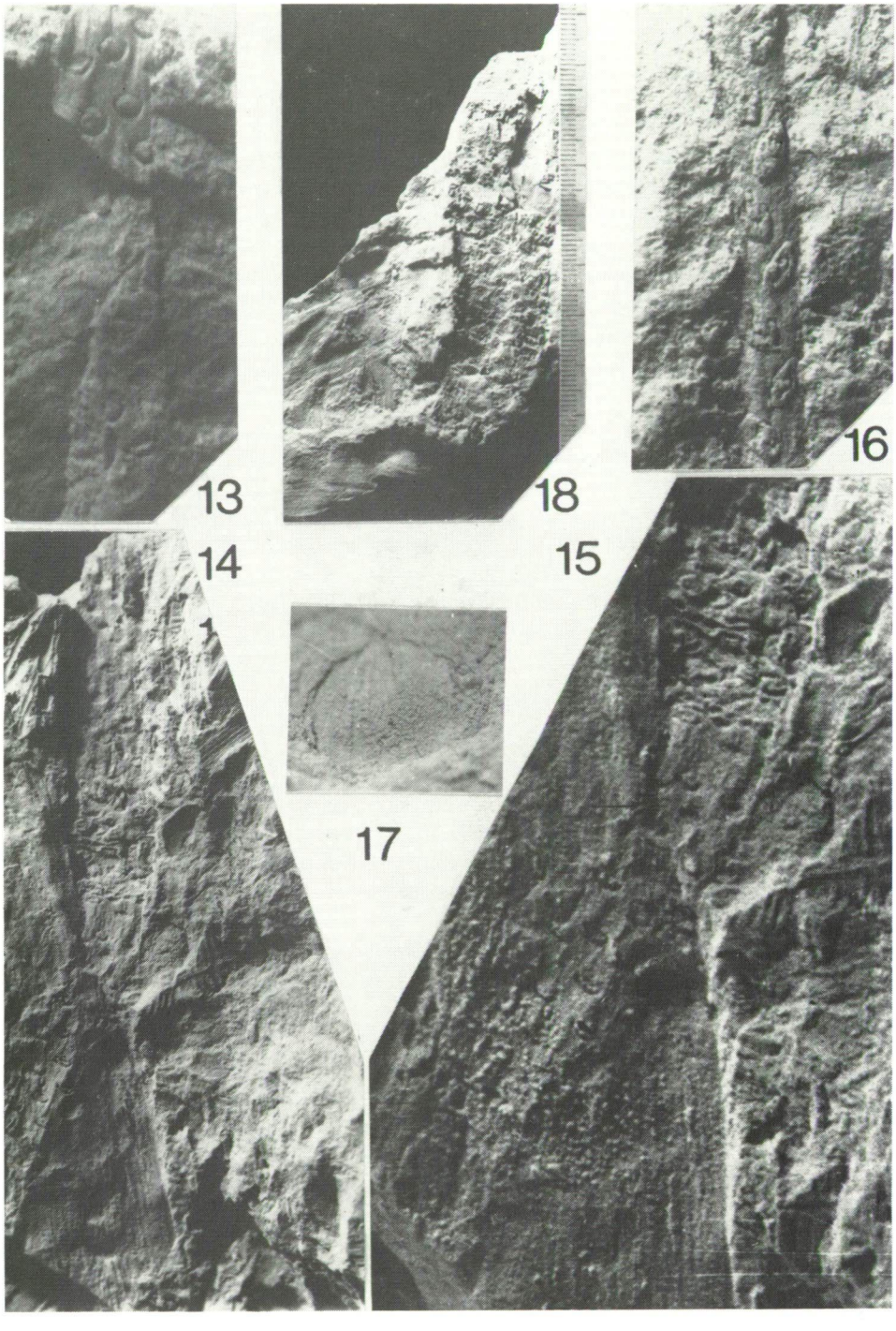
CONIFERALES

Pinus sp. (Plate 1.4., fig. 13—15, text-fig. 1.10.—1.12.)

The specimen shown in fig. 13, Plate 1.4., and text-fig. 1.10. represents an impression of a fragment of *Pinus* sp. stem. The fragment is 5 cm in length and about 6 mm broad. Dwarf shoot scars and crescent-shaped scars of subtending scale leaves

Plate 1.4. ►

13. *Pinus* sp. Impression of a stem fragment. Specimen H 64. Magnification ca 2 x.
14. *Pinus* sp. Impression of another stem fragment, showing scale zone at about the middle of the specimen and slightly broader than the rest of the stem. Specimen H 54. Magnification 1.2 x.
15. *Pinus* sp. The same, before revealing the portion of the stem above the broad zone of scales. Specimen H 54. Magnification ca 2 x.
16. *?Araucaria* twig showing prominent ?leaf scars. Specimen H 51. Magnification ca 2.5 x.
17. Seed or scale impression. Specimen H 41. Magnification 3.5 x.
18. Impression of a ?cone fragment. Specimen H 5. Magnification 0.7 x.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are clearly shown. The scar is 1.8 mm broad and 1.5 mm high. Figures 14 and 15 of Plate 1.4., and text-fig. 1.11. and 1.12. show another stem fragment most probably belonging to the same species of *Pinus*. The fragment is about 6 cm long and 6 mm broad.

It was first thought that the stem was terminated by a peculiar small head or cone as shown in fig. 15 of Plate 1.4., and text-fig. 1.12. However, on careful comparison with stems of similar size of extant *Pinus* species it became clear that the supposed cone corresponds to the zone of crowded rhomboidal scales usually present between long shoots of successive growing seasons. Accordingly, we "excavated" above the supposed cone and the remainder of the stem-fragment was revealed, as shown in Fig. 14 of Plate 1.4. and in text-fig. 1.11. This shows how far exact the agreement is between this fossil and extant *Pinus* species.

Fragment of an *?Araucaria* twig (Plate 1.4., fig. 16, text-fig. 1.13.)

An axis fragment under 5 cm in length and about 3 mm broad (Plate 1.4., fig. 16 and text-fig. 1.13.) is referred to *Araucaria* with hesitation. The axis bears more than 10 ?leaf cushions arranged in a regular manner. Every cushion has an elongate central ?leaf scar or bundle scar.

Fragment of a ?leaf (Plate 1.5., fig. 21, text-fig. 1.14.)

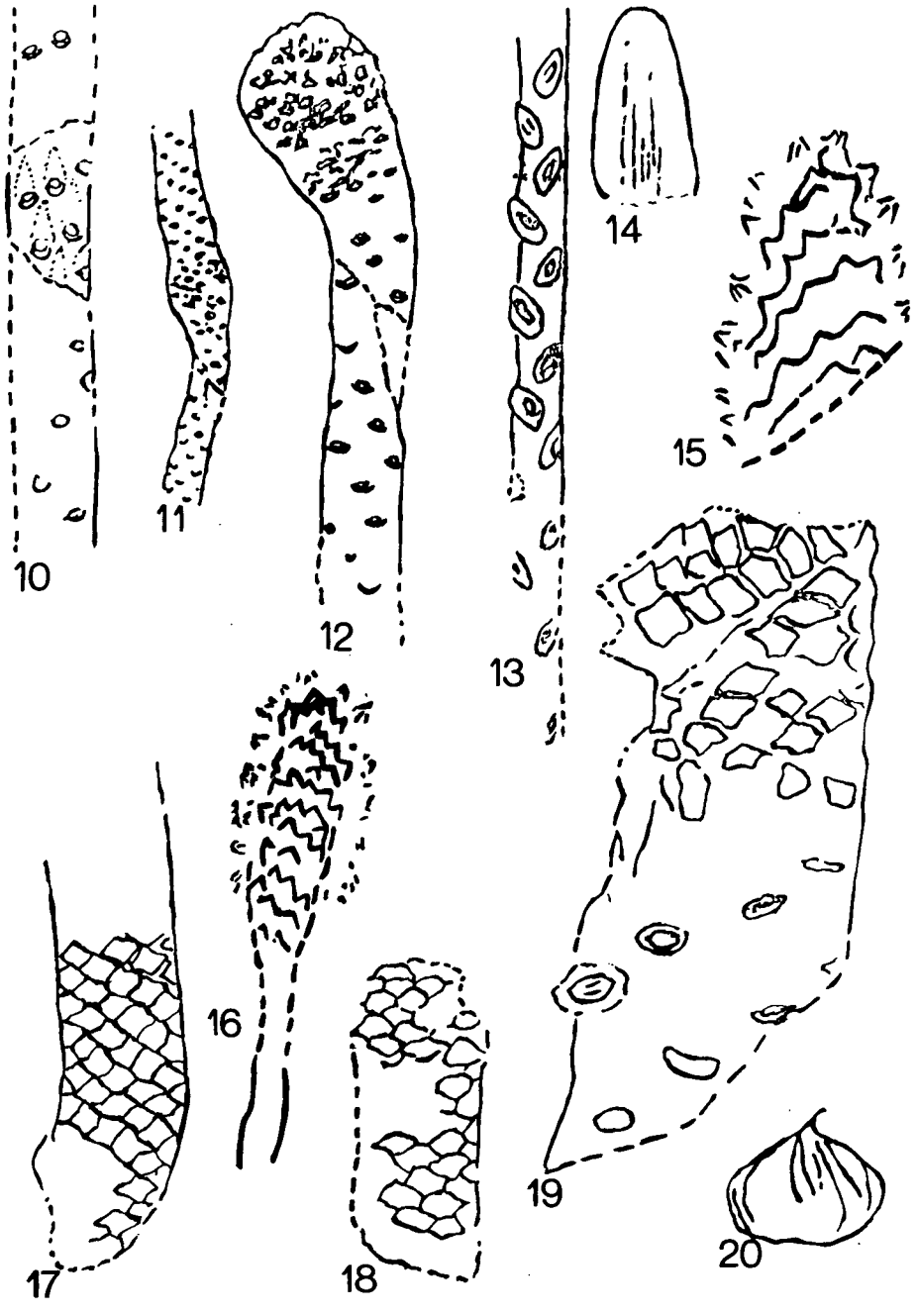
This ?leaf fragment is 3 cm long and 1.5 cm at broadest part. Longitudinal paralell lines probably represent leaf veins.

Impression of a cone (Plate 1.5., fig. 20, text-fig. 1.15., 1.16.)

Text-fig. 16 shows line drawing of cone found in slab No. H. 28. Portion of the counter part of this cone is shown in Fig. 20 of Plate 1.5., and text-fig. 1.15. The cone is about 5 cm long and 1.5 cm at the broadest part. The scales of the cone are spirally arranged. There are thin red coloured objects surrounding the cone. These objects perhaps represent delicate extensions of the cone scales. The preservation is not as good as in other associated fossils. This means that this cone was perhaps young; consisting of somewhat soft tissues. Other interpretations, however, are also possible.

Fragment of a ?cone (Plate 1.4., fig. 18, plate 1.5., fig. 19, text-fig. 1.17., 1.18.)

A fragment of a ?cone impression is shown in fig. 18 of Plate 1.4., and text-fig. 1.17. Its counter part is shown in fig. 19 of Plate 1.5., and text-fig. 1.18. The ?cone is about 5 cm long and 2 cm broad. The spirally arranged rhomboidal scars are horizontally extended being about 7 mm broad and 5 mm high. That this specimen represents an impression of a stem covered with persistent leaf bases is a probability which is not entirely excluded.



Text-figs. 1.10.—1.20.

1.10.—1.12. *Pinus* sp.
1.13. Fragment of an *?Araucaria* twig
1.14. Fragment of a ?leaf
1.15., 1.16. Impression of a cone
1.17., 1.18. Fragment of a ?cone
1.19. A stem fragment with a ?cone base attached
1.20. Impressions of seeds or ovuliferous scales

A stem fragment with a ?cone base attached (Plate 1.5., fig. 22, text-fig. 1.19.)

Plate 1.5., fig. 22 and text-fig. 1.19. show a stem fragment with spirally arranged leaf scars followed upwards by dense, spirally arranged rhomboidal scars. The stem is about 3 cm broad and 8 cm at longest part. The upper portion of the specimen, containing the rhomboidal scars, probably represents a cone base. Another possible interpretation is that this specimen represents a several years old conifer stem such as *Pinus*. In this case the upper portion of the specimen represents the zone of dense scales usually present between long shoots of successive growing seasons. At this zone also branching of the stem usually occurs in extant *Pinus* species.

Impressions of seeds or ovuliferous scales (Plate 1.4., fig. 17, text-fig. 1.20.)

Nine seed or scale impressions were met with in five specimens of the collection. One of these seeds (or scales) is shown on Plate 1.4., fig. 17, and text-fig. 1.20. The seed (or scale) is rounded or oval in shape. It is generally longer than broad but a single specimens was found to be broader than long (6×8 mm). The seed (or scale) is about 7.5 mm long and 5.5 mm broad. Extreme lengths recorded are 6 mm and 12 mm. Extreme breadths being 5 mm and 9 mm.

Comparisons

The above described specimens will now be compared with extinct and extant plants in the same order as they came in the description of the fossils.

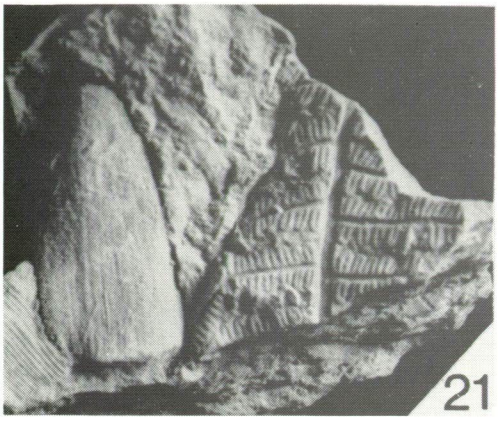
The two stem fragments referred to as *Pinus* sp. are identical with extant species of *Pinus*. The similarity is remarkable concerning: branch size, curvature, leaf and shoot scars, and the region of crowded rhomboidal scales etc...

The twig impressions referred to as *?Araucaria* is best compared with extant species of *Araucaria,* e.g. *A. bidwillii.* In this species defoliated branchlets have more or less the same shape, size and arrangement of leaf scars as in the fossil specimen concerned. There is also a probability that this fossil represents a cone axis that has shed its seeds.

The fossil specimen referred to as a ?leaf fragment does not offer much for comparison. However, we may mention the fossil *Ginkgoalian* leaf *Eretmophyllum lovisatoi* described by Edwards (1929a) from the Middle Jurassic of Sardinia as a possible material for comparison. Edward's specimen is, however, longer, and narrower than that of Abu Darag. Leaves of certain species of the extant genus *Agathis* may also be mentioned in this respect. Abu Darag's specimen may even represent a fragment of a cycadophyte pinna.

Plate 1.5. ►

19. Counter part of the specimen shown in fig. 18 of Pl. 1.4. Specimen H 5. Magnification 1.25 x.
20. The apical portion of a conifer cone. Specimen H 28. Magnification ca 2 x.
21. The apical portion of a ?leaf. Specimen H, (Kh) 3. Magnification 1.15 x.
22. Stem impression with a ?cone base attached. Specimen H 84. Magnification 1.35 x.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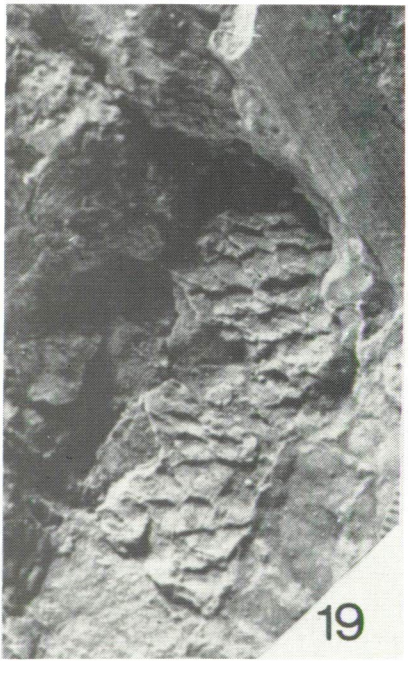
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The cone shown in text-fig. 16 is somewhat similar to *Tomaxiella biforme;* a female coniferous cone described and illustrated by ARCHANGELSKY (1968) from the Lower Cretaceous of Patagonia. *Picea excelsa;* a cone described and illustrated by SEWARD (1919) and SZAFER (1954) from Tertiary deposits and, *Pseudotsuga douglasii* a cone described and illustrated by POTONIÉ (1921) from Carboniferous strata are two examples resembling Abu Darag's cone to a certain degree.

The specimen referred to as a fragment of a ?cone (text-fig. 1.17., 1.18.) is somewhat similar in size and some other respects to the cone *Pinostrobus cylindroides* described and illustrated by MARIE STOPES (1915) from the Lower Cretaceous of Britain. It is also similar to the cone *Pinites dunkeri* as described and illustrated by CARRUTHERS (1866).

The specimen shown in text-fig. 1.19. and referred to as "a stem with a ?cone base attached" is comparable to several years old branches of extant *Pinus* sp. at their branching points as previously described. The upper portion of the fossil specimen may be compared also with the Jurassic cone *Araucarites sphaerocarpus* as illustrated by SEWARD (1919).

The nine impressions referred to as "seeds or ovuliferous scales" show great resemblances to ovuliferous scales and seeds of certain fossil plants. For example they are closely similar in size and shape to the Jurassic ovuliferous scale *Onthodendron florini (?Araucariaceae)* as described and illustrated by SAHNI and RAO (1933). Also to the Cainozoic cone scale *Doliostrobus* sp. *(Araucariacites gurnardi)* as illustrated by REID and CHANDLER (1926). They are also closely allied to the Jurassic fossil *Strobilites milleri* which is believed to be a seed (or a seed associated with scale) by SEWARD and BANCROFT (1913). The Jurassic coniferous seed *Allicospermum baiereanum* TRALAU (1966) is also allied to the fossils of Abu Darag.

Plant microfossils

The following samples were investigated palynologically:

Sample, No 1: comes from Early Cretaceous beds (Malha Formation), from North of Wadi El-Hommar, in the souther cliffs of El-Tih Plateau, Sinai.

Sample, No 5, and 6: come from Abu Darag (bed g of section H). Age of the bed is assumed to be Lower Cretaceous.

Reference number of sample No 5: H_{68}

Reference number of sample No 6: F_{12}

The geographical position of the samples investigated is represented on text-fig. 1.21.

Taxonomy of the plant micro-remnants

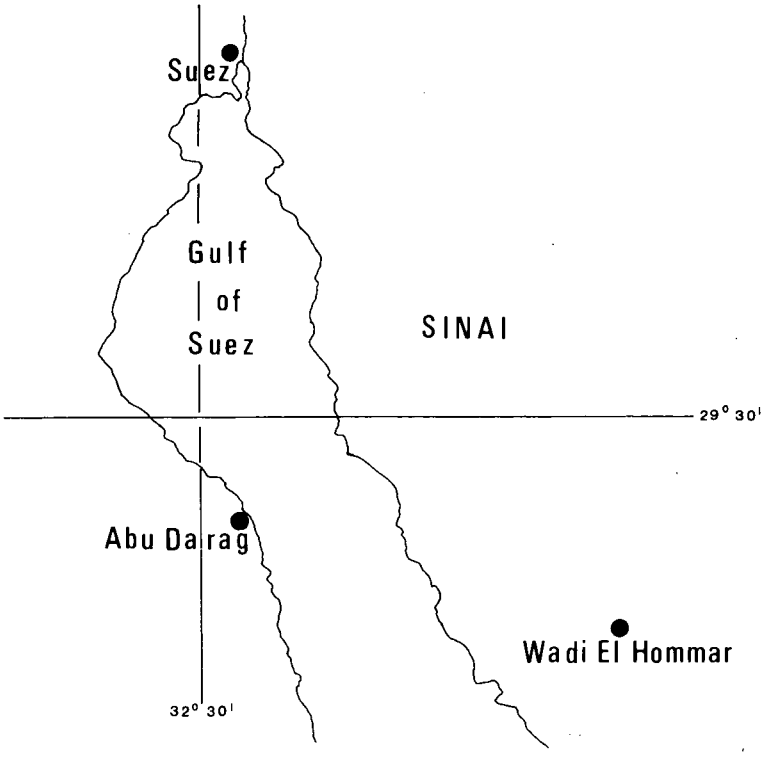
Spores

Fgen.: *Cyathidites* COUPER 1953

C. cf. *minor* COUPER 1958 (Plate 1.6., fig. 5, 6)

Fgen.: *Dictyophyllidites* COUPER 1958

D. harrisii COUPER 1958 (Plate 1.6., fig. 3,4)



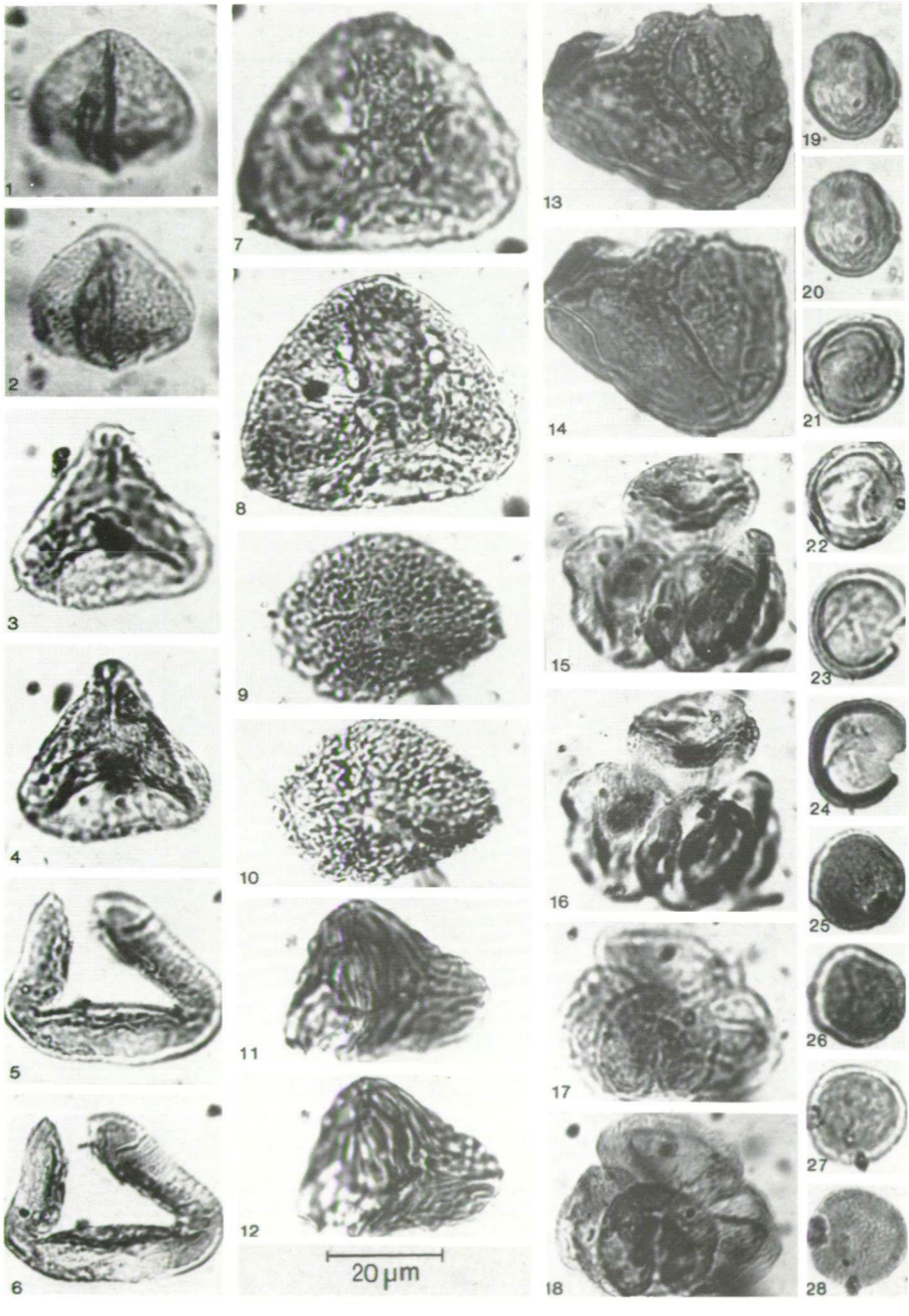
Text-fig. 1.21.

Sketch map showing the geographical position of the samples No 1, 5 and 6.

Fgen.: *Granulatisporites* (IBR. 1933) R. Pot. et. Kr. 1954
G. fsp. (Plate 1.6., fig. 9, 10)
Fgen.: *Vadaszisporites* DEÁK et COMBAZ 1867
Cf. *V.* fsp. (Plate 1.6., fig. 7, 8)
Fgen.: *Foveotriletes* (VAN DER HAMMEN 1954) ex R. POT. 1956
F. fsp. fvar. *triplan* (Plate 1.6., fig. 1, 2)
Fgen.: *Cicatricosisporites* R. POT. et GELL. 1933
C. venustus DEÁK 1963 (Plate 1.6., fig. 11, 12)
Fgen.: *Polypodiaceoisporites* R. POT. 1951
Cf. *P.* fsp. (Plate 1.6., fig. 13, 14)

Pollen grains

Fgen.: *Classopollis* PFLUG 1953
C. torosus (REISSINGER 1950) COUPER 1958 em. BURGER 1965 (Plate 1.6., fig. 15—18)
C. minor POCOCK et JANS. 1961 (Plate 1.6., fig. 17—20)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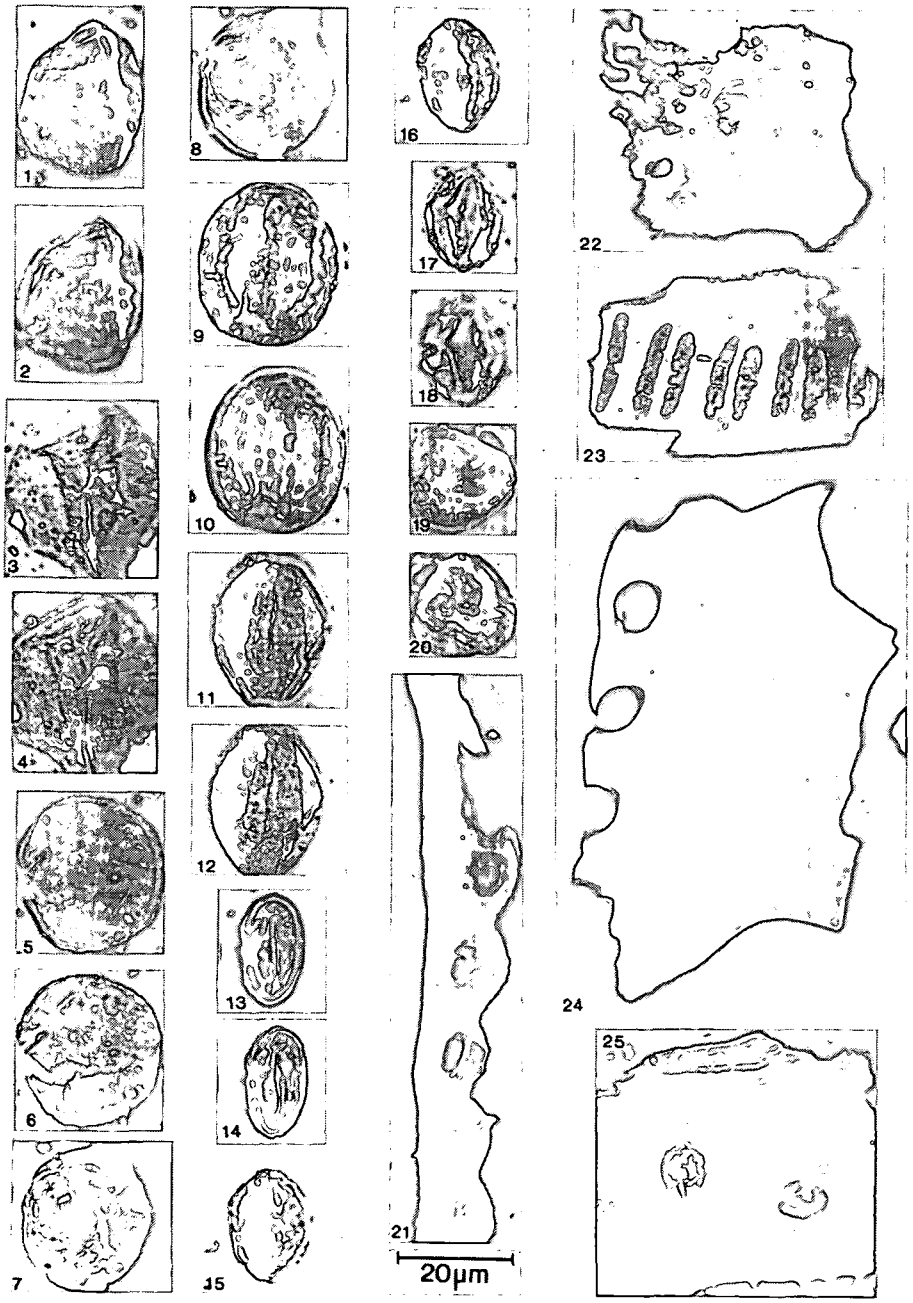
◀ Plate 1.6.

1,2. *Foveotriletes* fsp. fvar. *triplan,* slide: 1—1, cross-table number: 17.1/103.6.
3,4. *Dictyophyllidites harrisii* COUPER 1958, slide: 1—5, cross-table number: 99.0/113.6.
5,6. *Cyathidites* cf. *minor* COUPER 1958, *Cyatheaceae,* slide: 1—4, cross-table number: 19.7/103.9.
7,8. Cf. *Vadaszisporites* fsp., *Lycopodiaceae,* slide: 1—2, cross-table number: 7.6/118.2.
9,10. *Granulatisporites* fsp., slide: 1—5, cross-table number: 9.9/117.8.
11,12. *Cicatricosisporites venustus* DEÁK 1963, *Schizaeaceae, Anemia,* slide: 1—3, cross-table number: 17.6/111.1.
13,14. Cf. *Polypodiaceoisporites* fsp., cf. *Pteridaceae,* slide: 1—4, cross-table number: 10.0/105.5.
15,16. *Classopollis torosus* (REISSINGER 1950) COUPER 1958 em. BURGER 1965, *Cheirolepidaceae,* slide: 1—4, cross-table number: 8.9/113.2.
17,18. *Classopollis torosus* (REISSINGER 1950) COUPER 1958 em. BURGER 1965, *Cheirolepidaceae,* slide: 1—2, cross-table number: 10.2/107.3.
19,20. *Classopollis minor* POCOCK et JANS. 1961, *Cheirolepidaceae,* slide: 1—3, cross-table number: 8.6/112.7.
21,22. *Circulina parva* BRENNER 1963, *Cheirolepidaceae,* slide: 1—5, cross-table number: 18.2/111.3.
23,24. *Circulina parva* BRENNER 1963, *Cheirolepidaceae,* slide: 1—7, cross-table number: 16.9/117.4.
25,26. *Circulina parva* BRENNER 1963, *Cheirolepidaceae,* slide: 1—4, cross-table number: 16.7/118.1.
27,28. *Granuloperculatipollis* fsp., slide: 1—9, cross-table number: 4.3/112.6.

Fgen.: *Circulina* MALYAVKINA 1949
C. parva BRENNER 1963 (Plate 1.6., fig. 21—26)
Fgen.: *Granuloperculatipollis* VENK. et GÓCZ. 1964
G. fsp. (Plate 1.6., fig. 27, 28)
Fgen.: *Inaperturopollenites* (PFLUG 1953 ex TH. et PF. 1953) em. R. POT. 1958
I. dubius (R. POT. et VEN. 1934) TH. et PF. 1953 (Plate 1.7., fig. 1—4)
Fgen.: *Sigmopollis* HEDLUND 1965
S. fsp. (Plate 1.7., fig. 5—8)
Fgen.: *Eucommiidites* ERDTMAN 1948
E. troedssonii ERDTMAN 1948 (Plate 1.7., fig. 9—12)
Fgen.: *Cupuliferoidaepollenites* R. POT., THOMS. et THIERG. 1950
C. parvulus (GROOT et PENNY 1961) DETTMANN 1973 (Plate 1.7., fig. 13, 14)
C. cf. *parvulus* (GROOT et PENNY 1960) DETTMANN 1973 (Plate 1.7., fig. 15, 16)
Fgen.: *Retitricolpites* (Van der Hammen 1956) VAN DER HAMMEN et WIJMSTRA 1964
R. ecommoyensis LAING 1975 (Plate 1.7., fig. 17, 18)
Fgen.: *Triorites* (ERDTMAN 1947, COOKSON 1950) ex COUPER 1958 emend. R. POT. 1960
Cf. *Triorites* fsp. (Plate 1.7., fig. 19, 20)

Plant tissue remnants

Epidermis fragment of *Monocotyledonopsida* type (Plate 1.7., fig. 22)
Tracheids of *Pteropsida* type with scalariform pittening (Plate 1.7., fig. 23)
Gymnosperm secondary xylem fragments, tracheids with bordered pits (Plate 1.7., fig. 21, 24, 25)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◀ Plate 1.7.

1,2. *Inaperturopollenites dubius* (R. POT. et VEN. 1934) Th. et Pf. 1953, *Taxodiaceae* v. *Cupressaceae,* slide: 1—2, cross-table number 21.8/107.2.
3,4. *Inaperturopollenites dubius* (R. POT. et VEN. 1934) TH. et PF. 1953, *Taxodiaceae* v. *Cupressaceae,* slide: 1—1, cross-table number: 6.8/111.6.
5,6. *Sigmopollis* fsp., slide: 1—3, cross-table number: 20.9/108.9.
7,8. *Sigmopollis* fsp., slide: 1—1, cross-table number: 20.9/118.1.
9,10. *Eucommiidites troedssonii* ERDTMAN 1948, slide: 1—6, cross-table number: 5.2/105.3.
11,12. *Eucommiidites troedssonii* ERDTMAN 1948, slide: 1—2, cross-table number: 14.5/112.2.
13,14. *Cupuliferoidaepollenites parvulus* (GROOT et PENNY 1961) DETTMANN 1973, slide: 1—4, cross-table number: 4.6/113.6.
15,16. *Cupuliferoidaepollenites* cf. *parvulus* (GROOT et PENNY 1961) DETTMANN 1973, slide: 1—6, cross-table number: 17.1/113.2.
17,18. *Retitricolporites ecommoyensis* LAING 1975, slide: 5—10, cross-table number: 18.5/103,4.
19,20. Cf. *Triorites* fsp., slide: 1—2, cross-table number: 21.2/102.9.
21. Gymnosperm secondary xylem fragment, with bordered pits, slide: 1—2, cross-table number: 21.2/102.9.
22. Epidermis fragment of *Monocotyledonopsida* type, slide: 1—2, cross-table number: 19.9/114.2.
23. Tracheid of *Pteropsida* type with scalariform pitting, slide: 6—10, cross-table number: 14.3/108.7.
24. Gymnosperm secondary xylem fragment, with bordered pits, slide: 1—2, cross-table number: 12.1/111.7.
25. Gymnosperm tracheid fragment, with bordered pits, slide: 1—3, cross-table number: 21.6/108.5.

QUANTITATIVE DATA OF THE PLANT MICROFOSSILS

Sample No 1

Rich in plant microfossils, the spores and pollen grains are relatively well preserved. The greatest part of the enumerated and represented plant microfossils were observed in this sample. The quantitative data in the most important botanical groups are as follows:

	%
PTERIDOPHYTA	
Gleicheniaceae	2.5
Schizaeaceae	0.2
Varia	0.2
GYMNOSPERMATOPHYTA	
Inaperturopollenites dubius	25.0
"*Classopollis* group"	62.0
Eucommiidites troedssonii	6.9
ANGIOSPERMATOPHYTA	
Mostly *Longaxones*	0.2
INCERTAE	
Sigmopollis	3.0

Sample No 5

Very poor in sporomorphs. *Angiosperm* pollen grains *(Retitricolporites ecommoyensis)* and epidermis fragments of *Monocotyledonopsida* type were observed. The sample contains a great number of black coal fragments.

Sample No 6

The slides are rich in dark coloured, burnt plant tissue remnants. A very poorly preserved *Cyathidites* cf. *minor* was observed only.

INTERPRETATION OF PLANT MICROFOSSILS

1. The geological age of the samples, investigated on the basis of the spore-pollen assemblages, may be interpreted in different ways. The sample No 1 is without doubt of Lower Cretaceous age. The so-called Middle Mesozoic type spores and *Gymnospermatophyta* pollen grains *(Classopollis, Circulina, Eucommiidites)* together with the psilate and reticulate *Longaxones* angiosperm pollen grains refer to Aptian — Albian stage. The scarce *Brevaxones* pollen grains (cf. *Triorites*) is relatively younger in this respect. In Europe, the appearance of the first brevaxonate pollen grains is in the Upper Cenomanian. The plant micro-remnants of sample No 5, are a little problematical. The occurrence of *Retitricolporites ecommoyensis* refers to a Lower Cretaceous age. But the *Monocotyledonopsida* type epidermis fragment is unusual in this period. On the other hand, taking into consideration the new concepts of the evolution of the angiosperm pollen grains beside the early monosulcate type, the inaperturate one may also be presumed. The peculiar, angiosperm exine ultrastructure described from the nearly inaperturate Mesozoic gymnosperm pollen grain (*Spheripollenites scabratus* COUPER 1958) by KEDVES and PÁRDUTZ (1973) supports a so-called "inaperturate lineage" and also supports the polyphyletic evolution of the angiosperm pollen grains. ZAVADA (1984) published a new scheme about the most important evolutionary trends of the monocotyledonous pollen grains. The inaperturate type was derived from the monosulcate one. Here we propose to derive the inaperturate angiosperm pollen type from inaperturate gymnosperm pollen grains similarly to the monosulcate evolutionary lineage, e.g.: The early monosulcate pollen type originates from angiosperm pollen grains which are also of monosulcate morphology. In this way this early occurrence of the epidermis remnant of monocotyledonous type is not so surprising.

2. In connection with the ecological conditions of the sedimentation of the samples investigated it may be emphasized, that we have not observed hystrichosphaerids or such kind of micro-remnants which indicate salt water or brackish water conditions. In the reconstruction of the zonation of the vegetation it is only sample No 1 which contains a suitable quantity of sporomorphs. On the basis of the composition of the sporomorph a similarity may be established with the riparian vegetation of the Jurassic carbonate manganese ore layers published earlier (KEDVES and SIMONCSICS, 1964). The zonation was established as follows:

1. Open swamp, with *Pleurozonaria* = *Crassosphaeridae,* and *Hystrichosphaeridae.*
2. *Filicinae* zone.
3. *Cycadineae (Ginkgoinae)* zone.
4. *Cheirolepidaceae (Brachyphyllum, Cheirolepis, Pagiophyllum)* zone.
5. *Spheripollenites* producing *Coniferae* zone.

In our sample (No 1) the *Classopollis* type pollen grains is dominant, in this way, this refers to the *Cheirolepidaceae* zone. The important quantity of the inaperturate pollen grains refers to a *Taxodiaceae — Cupressaceae* zone, which may

be behind or before the *Cheirolepidaceae* zone. To solve this problem of the zonation we do not have up till now enough information.

3. Finally for the climate, the tropical fern spores *(Schizaeaceae, Gleicheniaceae)* may be mentioned.

General discussion

The conclusions based on the data of the plant macro- and microfossils are not always the same. This phenomenon was established several times by previous researchers. This phenomenon is related to the different conditions of the fossilization processes. In this place it is necessary to emphasize newly, that the chemical compounds of the leaves, fruits, seeds, spores and pollen grains are different, consequently diagenesis, selective fossilization and degradation are also different. To get the best interpretation we believe that it is one solution, to take the whole remnant matter together and synthetize their informations, and not interpret the macro- and micro-remnant assemblages in opposition. Every method has its advantages and disadvantages, the pluridisciplinary character of the palaeobotanical researches is a necessity.

Acknowledgements

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2. ILLUSTRATIONS OF THE QUASI-CRYSTALLOID BIOPOLYMER STRUCTURES FROM THE EXPLOSIVE DANGEROUS COAL PULVER

Short communication

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The first biopolymer units were observed in fossil exines from the Eocene sediments of Mississippi (U. S. A.) by KEDVES et al (1974). The quasi-crystalloid skeleton of the plant cell wall was first established in the partially degraded exine of *Pinus griffithii* MCCLELL. The idea of the possibility of getting a new energy basis by breaking the quasi-crystalloid skeleton was first mentioned by the author in 1987. On the other hand, the degradation of the organic material under natural conditions — sedimentation — may also discover the metastable quasi-crystalloid skeleton. This fossil biopolymer structure can be presented in the coal layers, too, in the mines under exploitation. The dry, finely granulous coal pulver containing a quasi-crystalloid skeleton may be explosive, liberating high energy. A research program was started with the coal pulver samples of Jurassic coal basin of the Mecsek Mountains. Some previous papers were published or are in print (KEDVES 1989a, b). Elaboration of the detailed results in under progress. In this paper a new method of illustration of the TEM picture of the explosion dangerous coal sample together with the results of the rotations are presented on one single plate. This kind of illustrations seems to be suitable to the necessary modifications for further biopolymer investigations of recent and fossil plant cell walls.

In plate 2.1. the gas channel is well shown in the coal particle. This is the very light part. The globular units of the quasi-crystalloid skeleton are also well shown. At the edges of the pentagonal polygon chosen for symmetry investigations are numbered. The rotation axis and the results of rotations are illustrated with the formula of the rotation. These latter mentioned pictures are oriented in the AP axis.

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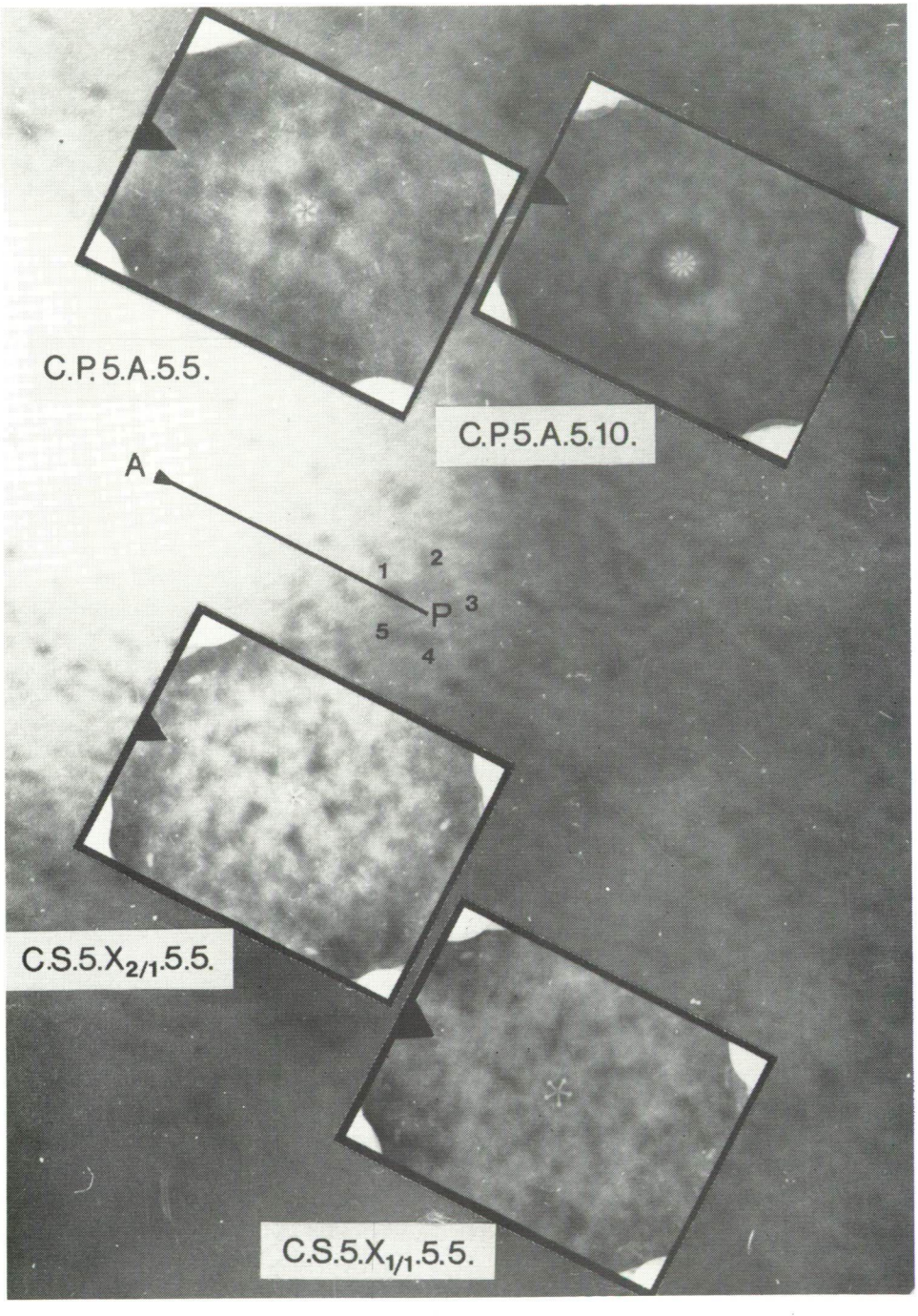

Plate 2.1.
Coal sample number: 148. Experiment No: 160, basic negative no. 7547. Magnification of all pictures: 500.000 x.

3. BASIS OF THE TERTIARY ROTATION AND TICOS MODELLING OF THE QUASI-CRYSTALLOID BIOPOLYMER SKELETON OF THE PLANT CELL

Short communication

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A short review concerning the discovery and the basic elements of the quasi-crystalloid skeleton of the partially degraded pollen exines is presented in paper No 4. The first methodical concepts and the most important first statements of TICOS modelling are also presented in this paper. The methodical elaboration with the first new results of the tertiary rotations was published a long time ago (KEDVES et al.). In this way it seemed to be important to present the basic statements of this kinds of rotations but by the developed form, and using the establishments of the results of TICOS modelling.

As it was emphasized in the paper under publication, after the demonstration of the so-called basic PENROSE-unit with the secondary rotation, "the further problem was evident: Is it a way to demonstrate the "second stage" of PENROSE-system (1979, p. 32, fig. 2) or at least space-equivalent organization from the biopolymer system of the plant cell wall" To get information about this problem the tertiary rotation method was elaborated. The basis for this kind of rotation is the scheme of a basic PENROSE-unit which resulted after a secondary rotation.

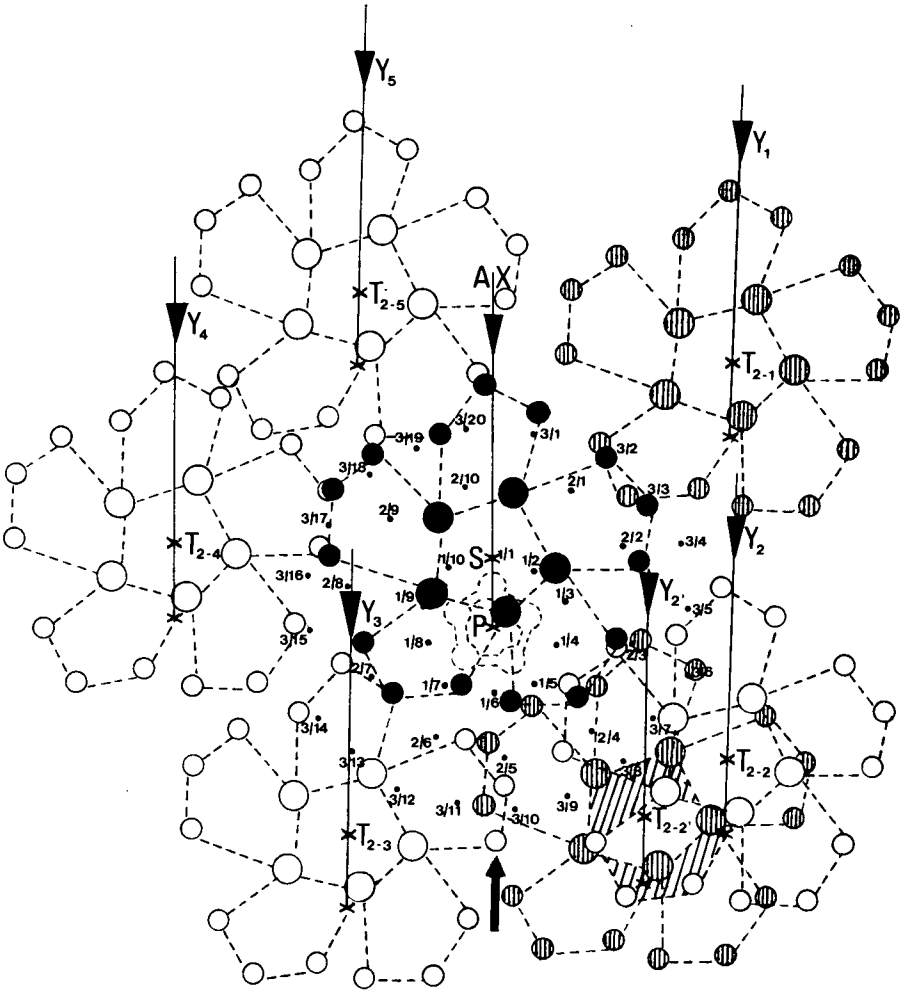
In text-fig. 3.1. we tried to join other PENROSE-like biopolymer units to the basic one taking our principles into consideration. The principle was the following:

1. The axes are parallel (Text-fig. 3.1.)
2. The two not perfectly connected points are as near as possible.

The first PENROSE-like biopolymer unit joined to the basic one fit defectively. We noticed our mistake and corrected it but we left it in the picture and indicated the first version by lining the little circles. The basic PENROSE-like biopolymer unit is black. The above mentioned mistake resulted that TICOS published in detail in the next communication bear this number. It is indicated by lining, too.

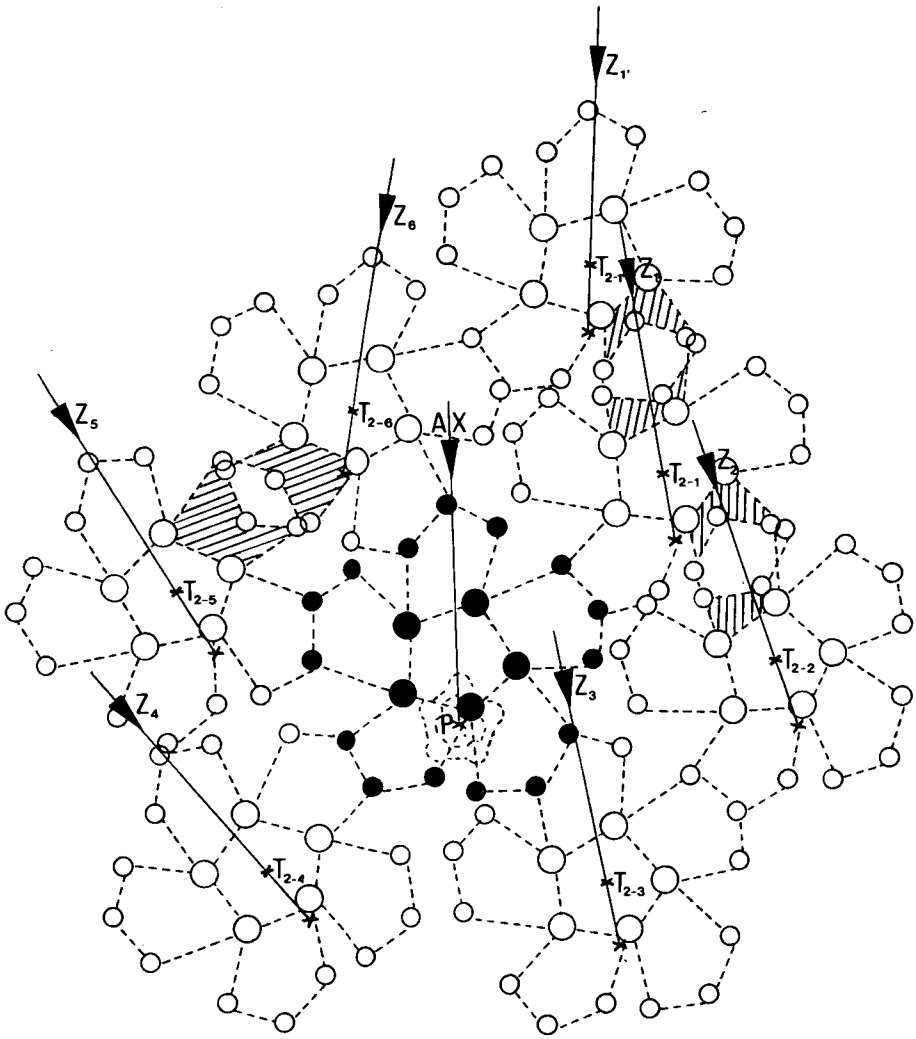
We can observe a TICOS under development marked with an arrow. This is produced by the above mentioned mistake.

In text-fig. 3.2. we joined the other PENROSE-like biopolymer units again to the basic one but the two points of contact covered each other perfectly. It resulted that the axes weren't paralell. In this case TICOS models were observed. We joined a sixth PENROSE-like biopolymer to the skeleton which produced a third TICOS. The three TICOS models are indicated by lining.



Text-fig. 3.1.

The basic PENROSE-like biopolymer is surrounded by five others. In this case the axes are parallel and the connection of the PENROSE-units is not perfect.

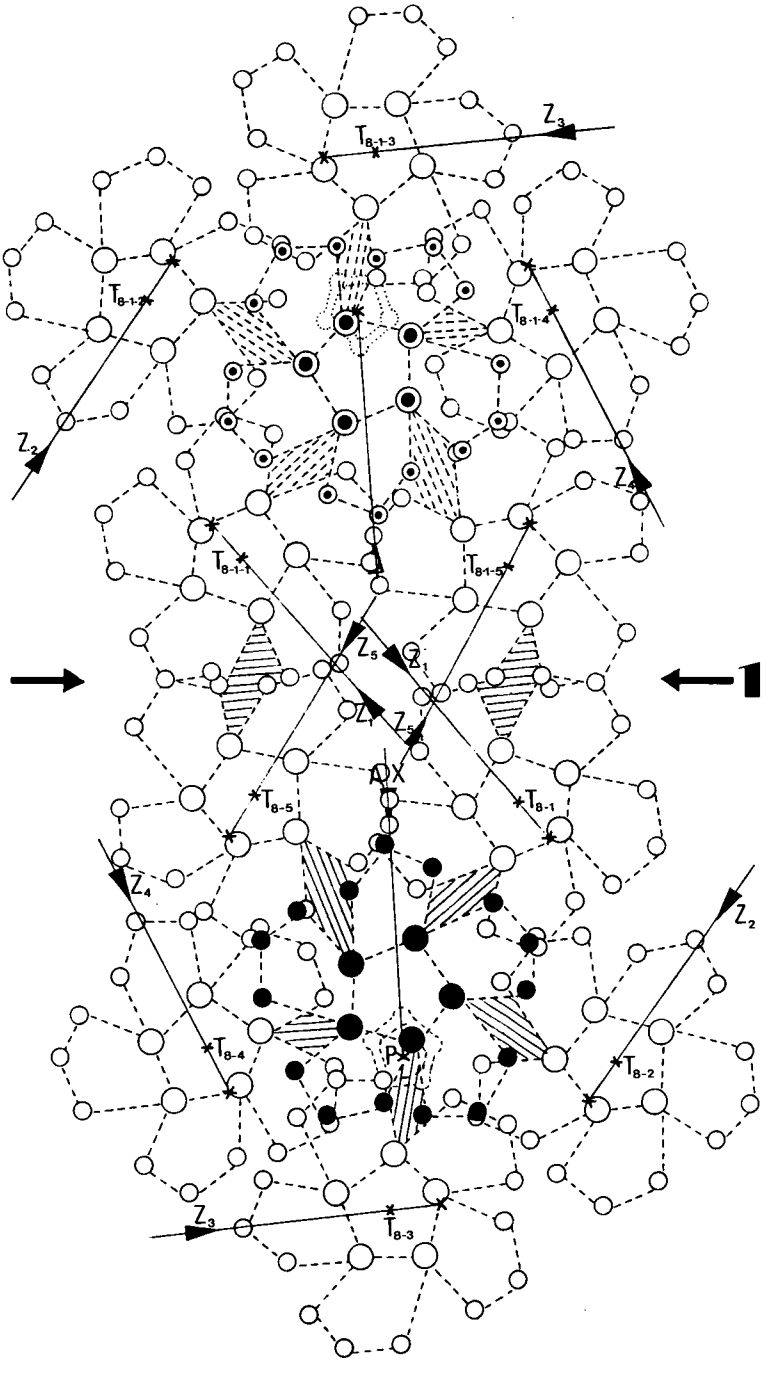


Text-fig. 3.2.

In this case the units cover each other perfectly and the axes are not parallel. Three TICOS models are produced.

Text-fig. 3.3.

The PENROSE-like biopolymer units are joined by four points of contact. It resulted in five rhombuses. Two whole skeleton is connected.


Z3
T8-1-3
T8-1-2
T8-1-4
Z2
Z4
T8-1-1
T8-1-5
Z5
Z1
Z1
Z5
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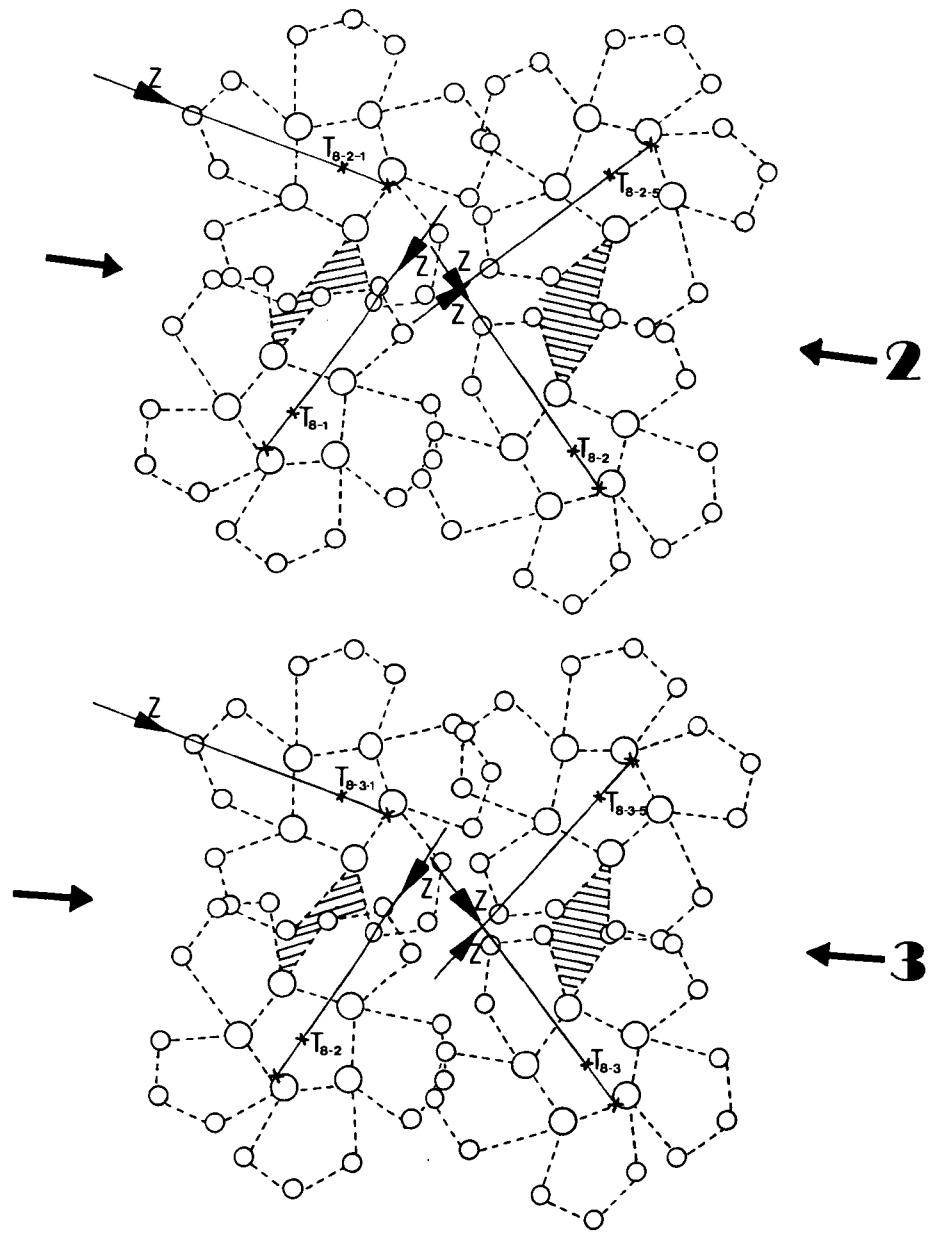
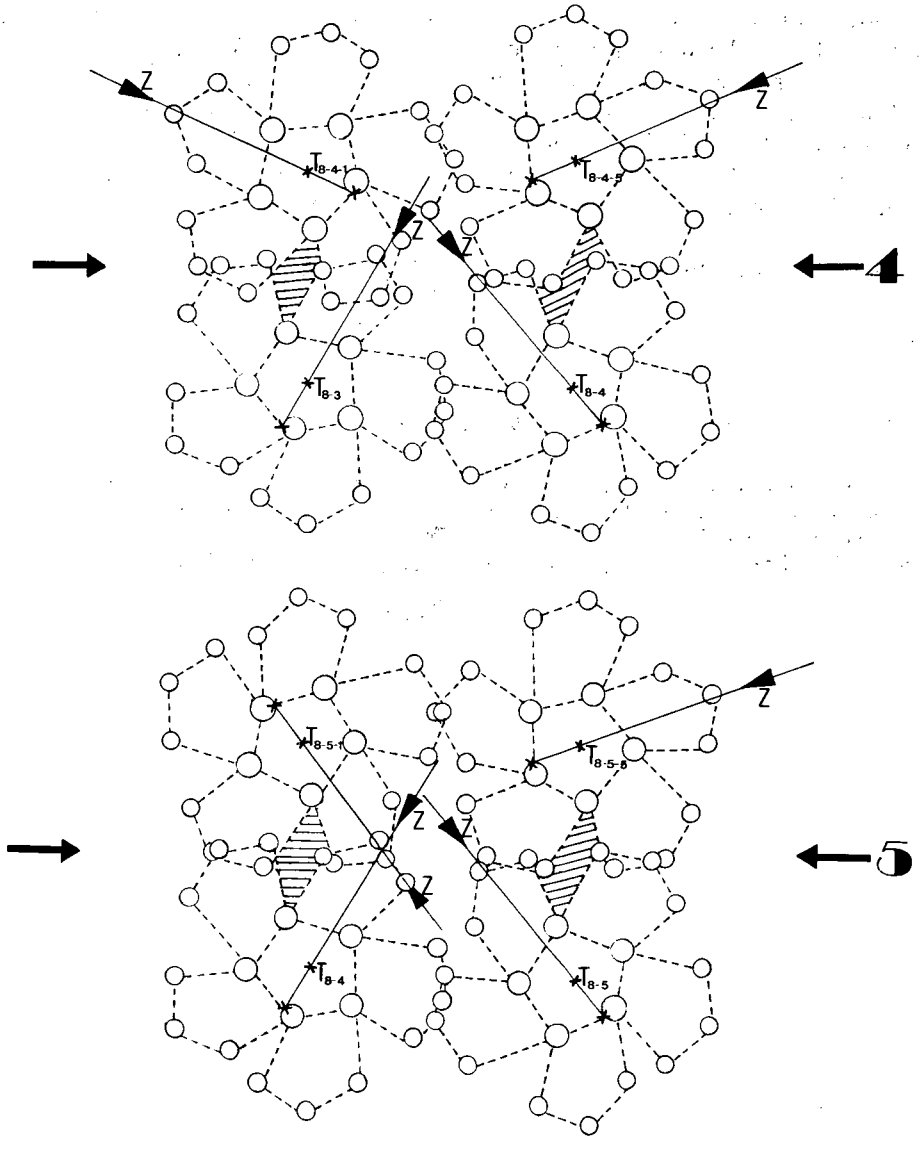
T8-5
T8-1
Z4
Z2
T8-4
T8-2
P
Z3
T8-3



Text-fig. 3.4.

It indicates the connection of the two skeletons at two skeletons at two more sides.



Text-fig. 3.5.

Two more kinds of joint can be seen in this scheme.

Our third examination resulted in text-fig. 3.3. In this picture we tried to get four points to cover each other. Of course it is impossible but they are as near as possible. This arrangement resulted five rhombuses marked by lining, too.

After this we joined a skeleton corresponding to the original to the above mentioned one. The number of the points of contact is eight. This attempt produced two more rhombuses indicated by lining. The joined skeleton is marked by spots in the little circles of its PENROSE-like basic biopolymer unit. It was performed at four more sides of the original skeleton (Text-fig. 3.4. and 3.5.). In the figures only the four connected PENROSE-like units of the skeletons are indicated. All of them produced the same result.

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4. TICOS POLYHEDRA AS A MODEL IN THE PENTASPORAN ORGANIZATION

Short communication

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During the TEM investigation of partially degraded exines as basic biopolymer units (pentasporan), pentagonal polygons were observed (cf. KEDVES, 1988, GÉVAY and KEDVES, 1989). Using the modified MARKHAM rotation method the following important statements were published, or are in print:

1. Justification of the regularity of the basic pentagonal biopolymer unit of the ectexine.
2. The first investigation system was published with several methods in 1989 by the writer (C = rotation complet, I = rotation incomplet, H = rotation complex, AP initial rotation axis, P = primary rotation, S = secondary rotation, A, B, X, Y, and Z are different kinds of rotation axes belonging to primary or secondary points of symmetries).
3. A PENROSE-like biopolymer structure was established by the way of secondary rotation. TEM picture of the quasi-periodically organized basic biopolymer skeleton was first published from the gymnosperm pollen wall in 1990 (KEDVES).
4. A further problem to resolve was finding symmetry operation method to get more PENROSE units and establish their connections. This "tertiary rotation" was elaborated by KEDVES et al., its basic methodical concepts can be seen in the previous paper. Detailed results are going to the published elsewhere.
5. As regards the details of the elaboration of the incomplete rotation this matter is under development.

Moreover several new research programs are in progress to get information about the biopolymer organization of the plant cell wall as much as possible. During the first investigations on the partially degraded intine of *Encephalartos ferox* BERTOL., a hexagonal basic biopolymer unit was established (KEDVES, 1991). Further hexagonal biopolymer structure was described from the outermost layer of *Selaginella bellula* MOORE (KEDVES, 1990b). In the above mentioned paper the following information was emphasized on page 587: "On the basis of the recently elaborated methods of the biopolymer organization of the sporoderm the hexagonal biopolymer organization may be modelled with the TICOS polyhedra." This paper summarizes the first basic statements in this respect, with remark that further ones will follow in all probability not so late. The whole matter was a part of the writer's contribution to the SAVITRI SAHNI SMARAK LECTURE in Lucknow on 19th September, 1990.

BURSILL and PENG JU LIN (1985, p. 51, fig. 3) published the schemes of the "Projection of crystalline Al_6Mn, showing edge-sharing of truncated icosahedra (TICOS) within layers and corner-sharing between layers."

The basic TICOS was applied for the biopolymer organization of the sporoderm with the following methods and results:

1. A scheme from the first observed pentagonal biopolymer unit was prepared. Its TEM pictures were first published by the writer in 1988b, p. 158, figs. 1–3 without rotation, fig. 4, after rotation; C. P. 5. A. 5.5. Two schemes of pentagon were placed in the opposite direction corresponding to the TICOS of BURSILL and PENG JU LIN (1985). The first surprising result was that two edges with globular elements appeared twice at the same place (Text-fig. 4.1.). In this way the TICOS model at the biopolymer unit resulted in a hexagonal polygon instead of icosahedra.

On the basis of this scheme new methodical elements must be introduced, too:

As regards the rotations centrums:

P = "Primary rotation: the centre of rotation is the middle of the biopolymer unit observed by direct TEM imaging" (as previously, p. 184, KEDVES, 1990).

P_{-5} = New notion for rotation. The centre of the opposite pentagon; in this case for a hypothetical pentagonal polygon biopolymer unit.

$P_{4,6}$ = The centre of the hexagon and a rhombus, which appeared after the modelling.

–A = The prolongated AP axis in negative province. In this case point "0" is equal with the basic P.

Axes of different kinds of rotations are indicated in the text-fig. 4.1. The results of different kinds of rotation are the following:

C.$P_{4,6}$.5.A.5.5. (Plate 4.1., fig. 1, text-fig. 4.1.)

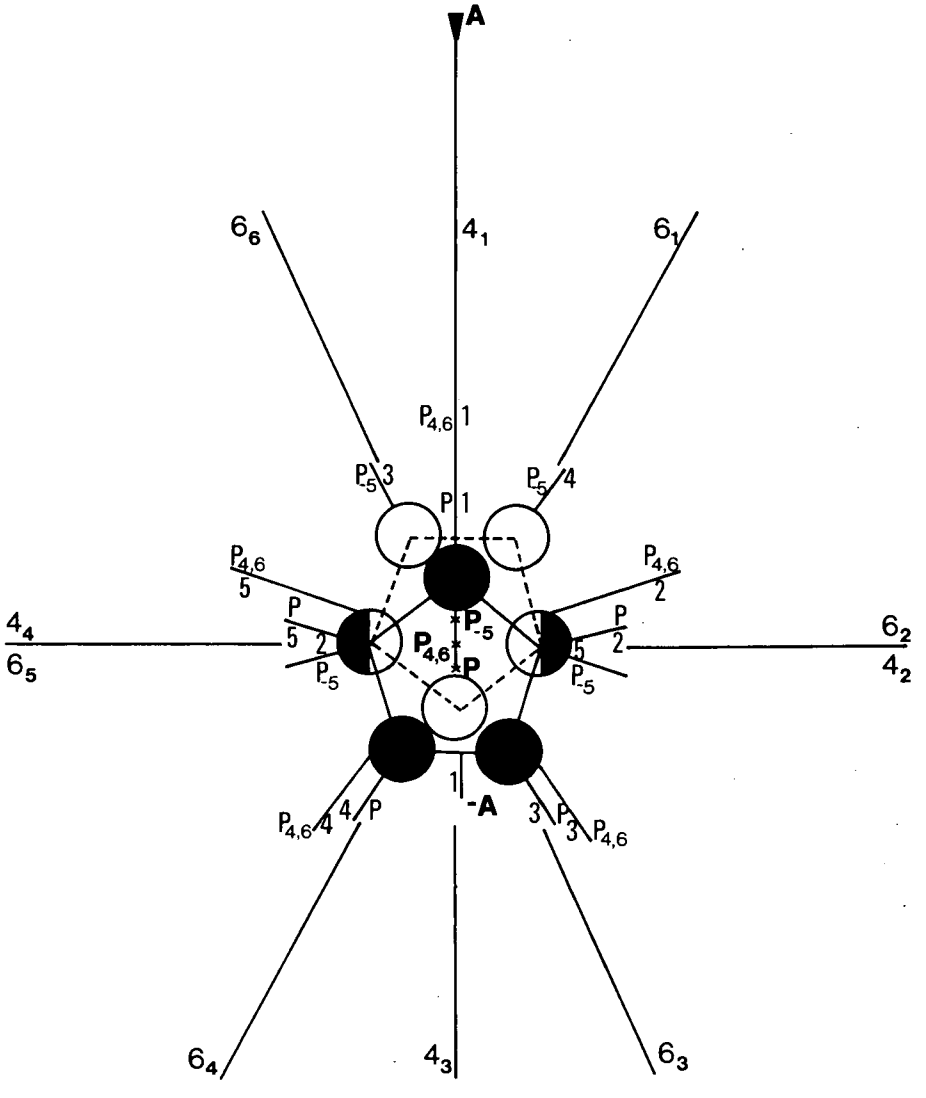
This kind of rotation was an attempt to the negative verification of the basic biopolymer unit. The rotation centre was not the centre of the biopolymer unit observed with direct TEM imaging, but the centre of the hypothetical rhombus, or hexagon. The difference is very little in Å but reinforced pentagon didn't appear after this rotation. This fact seems to be very important, because this is another argument which shows that our secondary and tertiary points of symmetries are not methodical artrefacts.

C.$P_{4,6}$.4.A.4.4. (Plate 4.1., fig. 2, text-fig. 4.1.)

This kind of rotation verified the rhombus arrangement of this biopolymer system. In the relation of the AP axis a partial reinforcing point may be seen at the 1., 2., and 5. globular edge of the basic biopolymer and at the opposite of the first one a hypothetical pentagon can be seen. The partial reinforcement is important because the centre of symmetry can be found in the middle of the "P" and "P_{-5}" centre. The secondary light tetragon and the further points of symmetries offer new supplementary rotation.

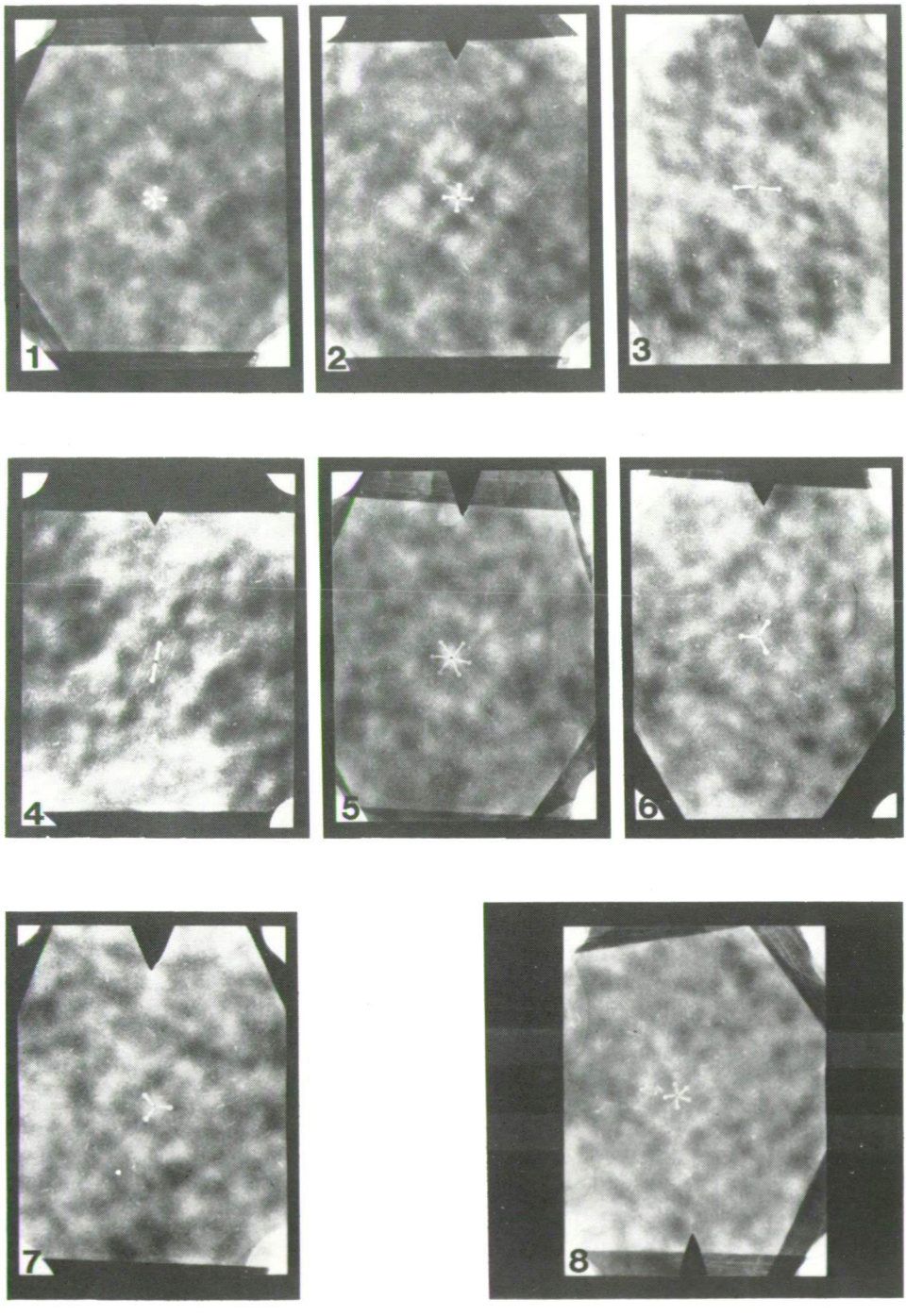
At this symmetry the two kinds of incomplete rotations were also made;

I.$P_{4,6}$.4.A.$4_{1,3}$.2. (Plate 4.1., fig. 3, text-fig. 4.1.)
I.$P_{4,6}$.4.A.$4_{2,4}$.2. (Plate 4.1., fig. 4, text-fig. 4.1.)



Text-fig. 4.1.

Scheme of the basic TICOS model applied to the basic biopolymer unit of the partially degraded exine of *Pinus griffithii* McCLELL.


1
2
3
4
5
6
7
8

◀ Plate 4.1.

Pinus griffithii McCLELL basic biopolymer unit after rotation.
1. $C.P_{4,6}.5.A.5.5.$
2. $C.P_{4,6}.4.A.4.4.$
3. $I.P_{4,6}.4.A.4_{1,3},2.$
4. $I.P_{4,6}.4.A.4_{2,4},2.$
5. $C.P_{4,6}.6.4_{1-6}.6.$
6. $I.P_{4,6}.6.A.6_{1,3,5}.3.$
7. $I.P_{4,6}.6.A.6_{2,4,6}.3.$
8. $C.P_{-5}.O.-A.5.5.$
Magnification: 500.000 x.

Indexes 1,3 and 2,4 indicate the numbers of globular units. One of them, 4_3 is hypothetical.

Characteristic secondary points of symmetry appeared. The patterns of these secondary points of symmetry are different. But especially characteristic ones are presented on Plate 4.1., fig. 4.

$C.P_{4,6}.6.A_{1-6}.6.$ (Plate 4.1., fig. 5, text-fig. 4.1.)

The hexagons which are not so characteristic (inner dark and outer bright) represent the biopolymer TICOS symmetry of pollen exine probably well. In this case the incomplete rotations were also made;

$I.P_{4,6}.6.A.6_{1,3,5}.3.$ (Plate 4.1., fig. 6, text-fig. 4.1.)
$I.P_{4,6}.6.A.6_{2,4,6}.3.$ (Plate 4.1., fig. 7, text-fig. 4.1.)

Two opposite biopolymer structures of triangular arrangement appeared after these two kinds of incomplete rotations. Finally the most interesting and important rotation was probably the following;

$C.P_{-5}.O.-A.5.5.$ (Plate 4.1., fig. 8, text-fig. 4.1.)

The regular opposite pentagonal polygon appeared as a result of this kind of rotations. In this way the supposed opposite polygon was verified. "O" means that there is no direct TEM information about this pentagon.

This short communication may be taken as a preliminary result, several further ones are going to follow this paper.

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5. INVESTIGATIONS ON THE BASIC BIOPOLYMER STRUCTURE OF THE ECTEXINE OF ALNUS GLUTINOSA (L.) GAERTN.

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Abstract

Partially degraded exines of *Alnus glutinosa* (L.) GAERTN. were investigated with the TEM method. The quasi-crystalloid biopolymer lattice was discovered in angstroem dimension and was investigated in ultrathin sections. Several kinds of the modified Markham rotation method were used to verify and investigate the symmetry of the basic polygon. Complementary elements of the methods are also introduced in this paper.

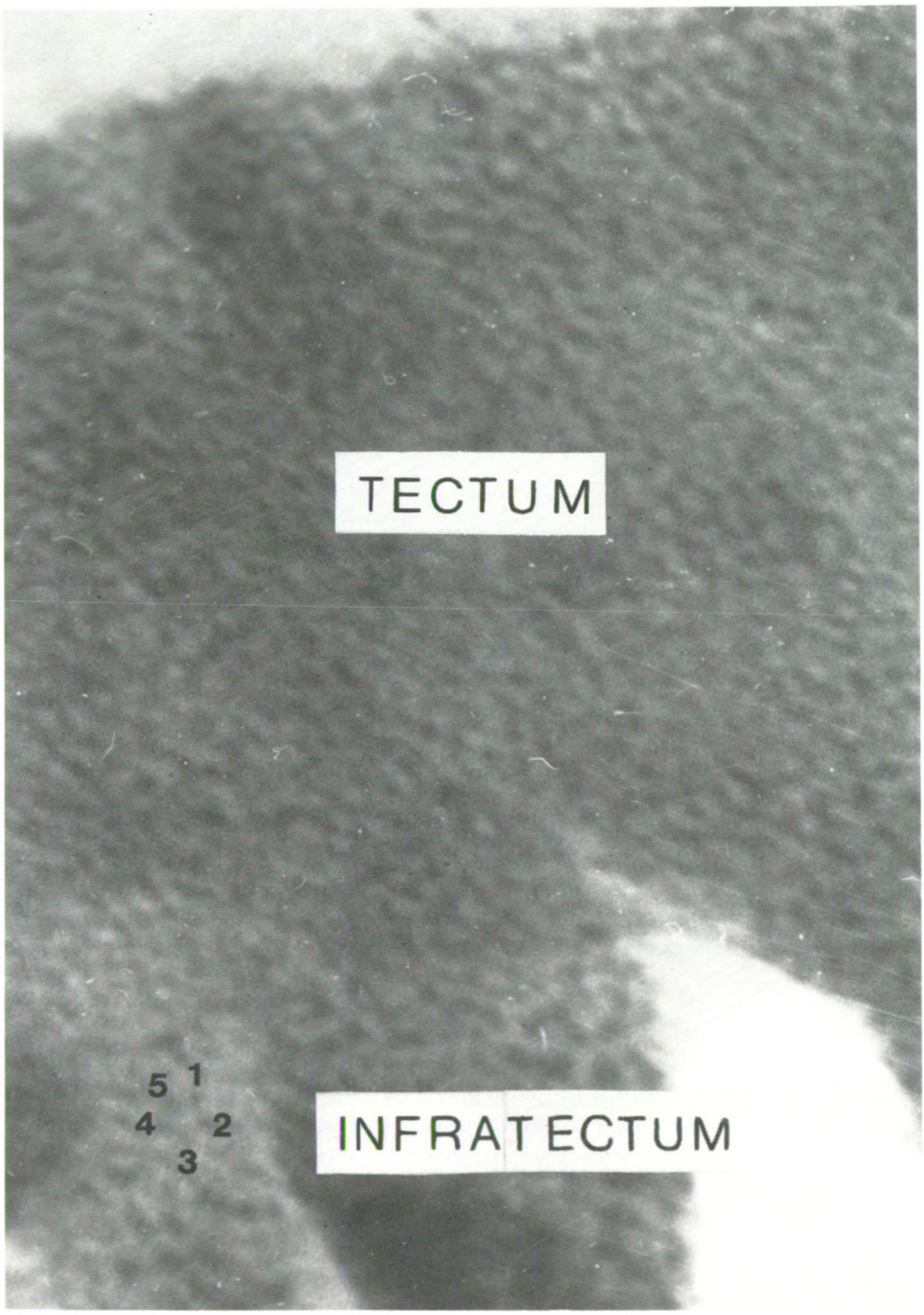
Key words: Palynology, *Angiospermae, Alnus,* biopolymer organization.

Introduction

After several data about exine sub-units published in previous publications (e. g.: ROWLEY et al., 1981, SOUTHWORTH, 1986), the quasi-crystalloid character of the basic biopolymer units of the sporoderm was published first in 1988 by KEDVES. This first observation was followed by detailed methodical and enlarged research program. We urgently needed data on angiosperm exines and other kinds of plant cell walls because the first investigations were made on gymnosperm exines. Several methodical, molecular structural and biopolymer evolutionary studies are under development. To use the fragmentation method of the partially degraded exines the pollen grains of *Alnus glutinosa* (L.) GAERTN. were chosen for the first attempt (KEDVES and ROJIK 1989).

The purposes of the present investigations are the following:

1. To get information about the biopolymer organization of the partially degraded wall and angiosperm pollen grain with the transmission electron-microscope method.
2. The rotation methods were used on basic biopolymer units inside of the partially degraded wall in contrast to the first observed biopolymer unit of the exine of *Pinus griffithii* MCCLELL.
3. To compare the obtained results with the previous ones, particularly with data of the fragmentation method of this species.
4. To use critically the above mentioned methods and to modify or complete them if necessary.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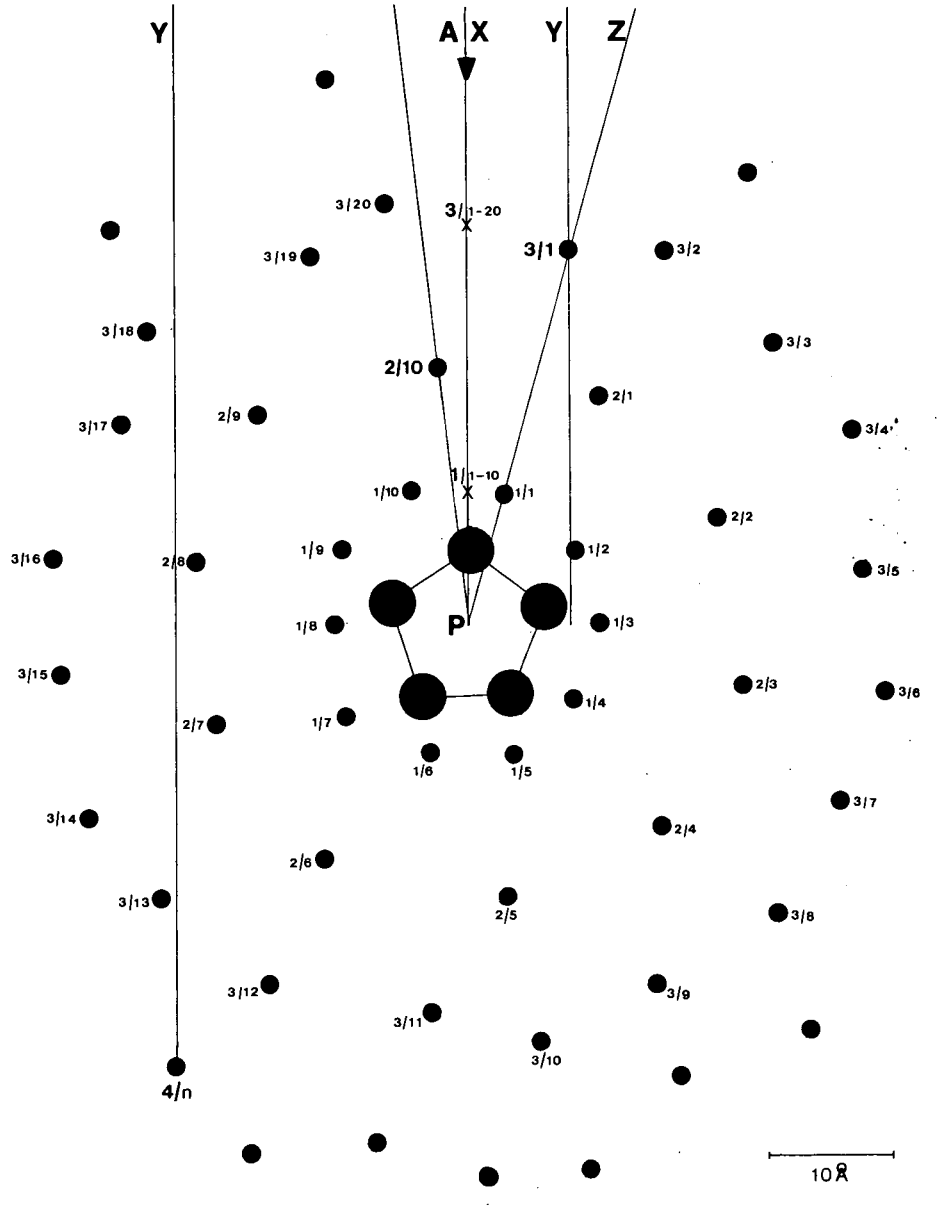
INFRATECTUM

◀ Plate 5.1.

Alnus glutinosa (L.) GAERTN., partially degraded exine. The numbering of the globular elements at the edges indicates the biopolymer unit for symmetry investigations. Experiment No 226. Negative no: 8349, 500.000 x.



Text-fig. 5.1.

Schema of the biopolymer and secondary points of symmetry after rotation C.P.5.A.5.10., and the axes.

Materials and Methods

The material of investigation was collected by Dr. K. MARGÓCZY on 25th February, 1989, in the Botanical Garden of the J. A. University. The freshly collected material was frozen at 20 °C below zero. The experiment was made on 28th May in 1988 as follows. We mixed 20 mg air dried pollen grains to 1 ml 2—aminoethanol at a temperature of 30°C for 24 hours. Then we washed it with distilled water and added 10 ml $KMnO_4$ aq. dil. at a temperature of 30 °C for 24 hours length of time. After washing it, the partially degraded exines were fixed in OsO_4 aq. dil. and embedded in Araldite (Durcupan, Fluka). The ultrathin sections were made by a Porter Blum ultramicrotome with glass knives in the Electron Microscopical Laboratory of the Department of Biophysics of the Hungarian Academy of Science. The TEM pictures were made by a BS Tesla—500 transmission electron microscope in the Laboratory of Electron-microscopy of the Faculty of Sciences of the J. A. University. We express our sincere thanks to Dr. I. ROJIK for his technical assistance.

Results

TEM picture of Plate 5.1. well represents the results of the partial degradation of the pollen grain. The elements of the quasi-crystalloid lattice of the tectum (pro parte) and a part of the infratectal layer (infratectum) are illustrated. The molecular and biopolymer pecularities of the surface were not investigated during this experiment. The pentagonal polygon basic biopolymer unit was chosen at the upper part of the infratectum for symmetry investigations with the modified MARKHAM rotation method. The numbering of the globular elements at the edges indicates the AP axis, too ("A — a linear feature between the centre of the actual biopolymer and one apex of the biopolymer polygon", KEDVES 1990, p. 184). This apex is marked with number "1" every time. On that account this apex was not indicated in this picture. The scheme of the modified MARKHAM rotation operations and the secondary points of symmetries are illustrated in text-fig. 5.1.

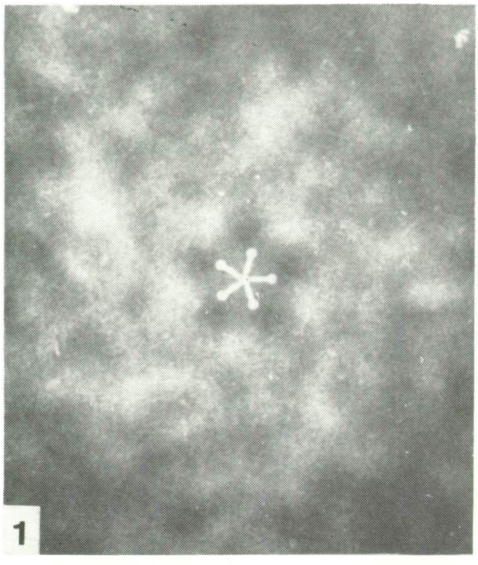
1. THE RESULTS OF THE PRIMARY ROTATIONS

C.P.5.A.5.5. (Plate 5.2., figs. 1, 3, 6, 7 and 8)

This kind of basic rotation was repeated six times for basic methodical purposes in this case. The reason of this numerous repetitions was that this basic biopolymer unit is structural and it can be found not at the border of the disintegrated biopolymer lattice as at *Pinus griffithii* MCCLELL. From these rotations we present three ones. Figs. 1, 2 in Plate 5.2. represent the best — we can say the perfect — result. This was taken as a basis for the further investigations. The shadow of the pin

Plate 5.2. ►

Alnus glutinosa (L.) GAERTN.
The basic biopolymer unit after rotation.
1. Rotation: C.P.5.A.5.5., x 1 Million.
2. Rotation: C.P.5.A.5.10., x 1 Million.
3., 6., 7., 8. Rotation: C.P.5.A.5.5., 500.000 x.
4., 5. Rotation: C.P.5.A.5.10., 500.000 x.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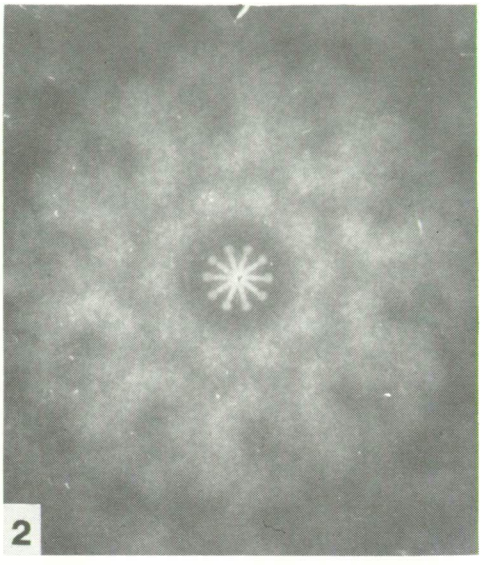
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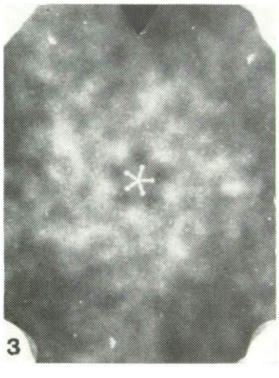
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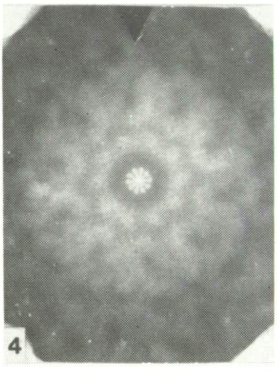
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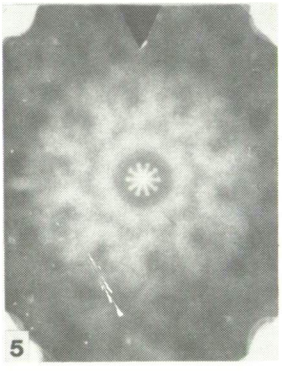
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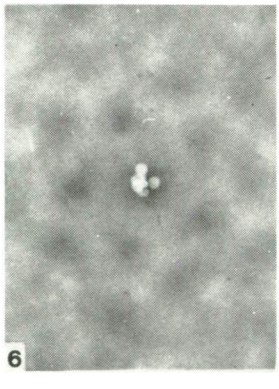
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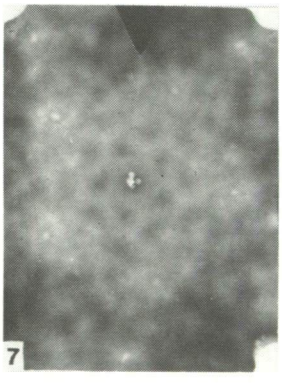
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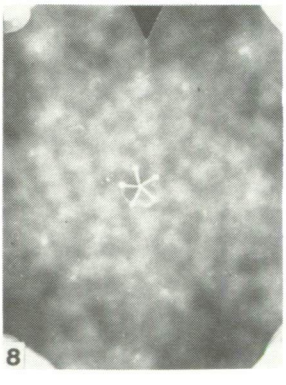
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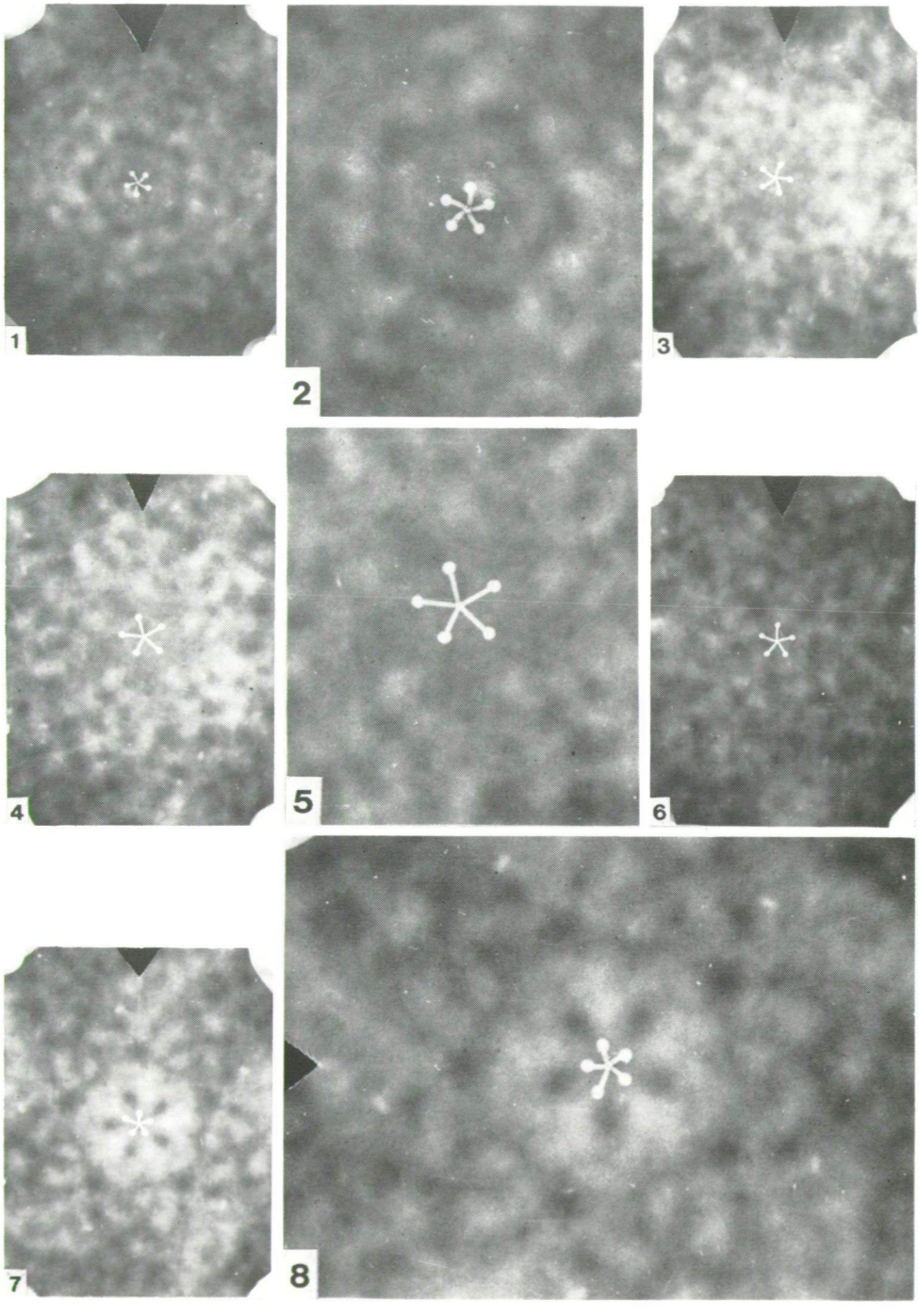
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◀ Plate 5.3.

Alnus glutinosa (L.) GAERTN.
The basic biopolymer unit after rotation.
1., 3. Rotation: C.S.X.1/1—10.5.5., 500.000 x.
2. Rotation: C.S.X.1/1—10.5.5., x 1 Million.
4., 6. Rotation: C.S.Z.2/10.5.5., 500.000 x.
5. Rotation: C.S.Z.2/10.5.5., x 1 Million.
7. Rotation: C.S.X.3/1—20.5.5., 500.000 x.
8. Rotation: C.S.X.3/1—20.5.5., x 1 Million.

fixing the photograph paper also serves valuable information. In figs. 6, 7, the fixation of the centre was not strong enough during the rotation. This "defective" attempt seems to serve not also neglectable information as it is well illustrated in Plate 5.2., fig. 7. In this case the connecting PENROSE-like units may be recognized. It is interesting that the results of a completely different, not really well rotation are essentially similar — it is illustrated in Plate 5.2., fig. 8.

In consequence another important methodical question emerged: that the secondary points are outside the AP axis. This probably results from the position of the pentagonal polygon biopolymer unit.

C.P.5.B.5.5 rotation seemed to be not necessary in this case.

C.P.5.A.5.10. (Plate 5.2., figs. 2, 4, 5)
This was also repeated twice. In detail some differences are illustrated in figs. 4. and 5.

2. RESULTS OF THE SECONDARY ROTATIONS

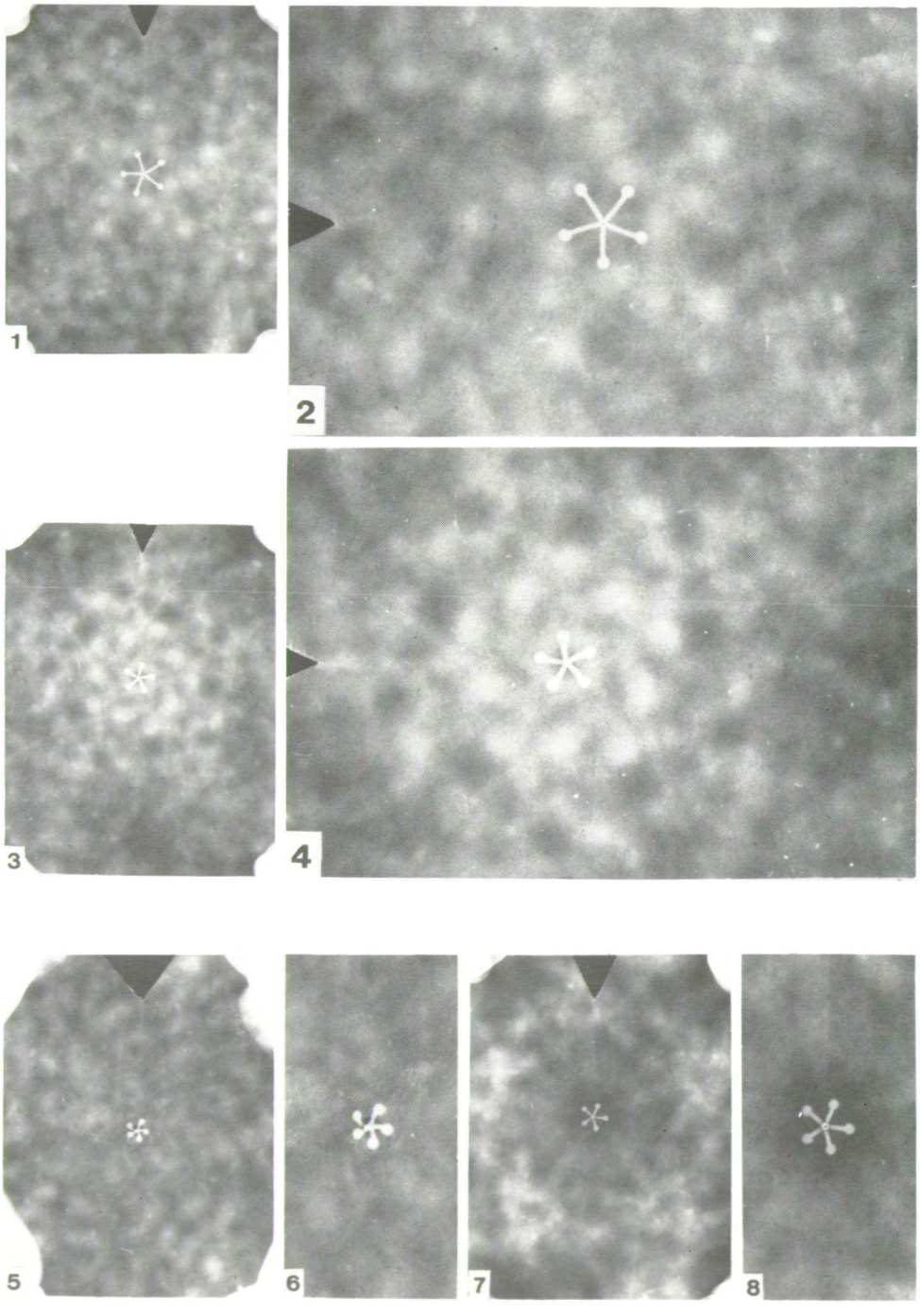
Taking into consideration the previous results, all kinds of rotations were repeated twice.

As new methodical establishments the following can be pointed out:

In the case when the PA = PX axis doesn't cross the secondary point, "theoretical" rotation points can be marked out. This is the crossing point of the circle line of the secondary symmetry points and the PX axis. This point is indicated by the first and last biopolymer of the circle, e.g.: 3/1—20 indicates the point between the first and the 20th secondary points of the third circle.

When it is impossible to count the points of symmetries (the circle is not complete) then the point is indicated with "n" after the number of the circle. In this cases this secondary point is the centre of this kind of rotations. We have to emphasize that in such a case a scheme is obligatory.

C.S.X.1/1—10.5.5. (Plate 5.3., figs. 1—3, text-fig. 5.1.)
Minor mistakes are causally made during the rotations. The shadows of the pin well indicate this phenomenon. Regarding the details there are differences but characteristic larger pentagons have appeared. Particularly picture 3 represents well the points of symmetry. The axis intersects the line connecting the two apexes of the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◀ Plate 5.4.

Alnus glutinosa (L.) GAERTN.
The basic biopolymer unit after rotation.
1. Rotation: C.S.5.Z.3/1.5.5., 500.000 x.
2. Rotation: C.S.5.Z.3/1.5.5., x 1 Million.
3. Rotation: C.S.5.Y.3/1.5.5., 500.000 x.
4. Rotation: C.S.5.Y.3/1.5.5., x 1 Million.
5—8. Rotation: C.S.5.Y.4/n.5.5.
5. 500.000 x.
6. x 1 Million.
7. 500.000 x.
8. x 1 Million.

large pentagon. It is worth mentioning that numerous secondary points can be investigated which are pro parte dark or light. Of course, these secondary points open new chance of further symmetry operations.

C.S.Z.2/10.5.5. (Plate 5.3., figs. 4—6, text-fig. 5.1.)

As regards the methodical situation this is the same as previously described. But at the case of both rotations illustrated in figs. 4 and 6, Plate 5.3., the appeared points of the PENROSE-like biopolymer arrangement can be recognized. This biopolymer organization is well illustrated in fig. 4., Plate 5.3. Further characteristic secondary points of symmetry have appeared.

C.S.X.3/1—20.5.5. (Plate 5.3., figs. 7, 8, text-fig. 5.1.)

In the direction of the left hand oriented peculiar pentagon was reinforced. Around this pentagon a large light pentagonal structure has appeared. Round the light structure numerous supplementary points of symmetry can be observed. The PENROSE-like arrangement is to be recognized, too.

For the point of symmetry 3/1 we have made two kinds of rotations: the "Y" and the "Z" as well.

C.S.5.Z.3/1.5.5. (Plate 5.4., figs. 1, 2, text-fig. 5.1.)

In the figs. 1, 2, of Plate 5.4. the two larger pentagons are well shown. The globular units of the light one are oriented at the rotation axis. The orientation of the dark pentagon is slightly in the left hand direction. There are several further new characteristic points of symmetry — light and dark as well.

C.S.5.Y.3/1.5.5. (Plate 5.4., figs. 3, 4, text-fig. 5.1.)

A remarkable difference can be established in contrast to the previous kind of rotations. Three characteristic pentagons have appeared, which are arranged concentrically. The inner one is composed of five dark points of symmetry. The following is light and ten points can be counted. Another large dark pentagon follows this. At the apices of this pentagon further units can be observed in pentagonal arrangement.

C.S.5.4/n.5.5. (Plate 5.4., figs. 5—8, text-fig. 5.1.)

These points of symmetry are the farthest ones from the basic "P" point. It is well-shown that the rotation illustrated in pictures 5,6 is not completely perfect. Peculiar and interesting pentagons have appeared; dark points surrounded by light circles. The approximatively perfect rotation has resulted interesting pentagons with straight sides.

General conclusions

1. The pentagonal polygons becoming regulated in the structure in the inner part of the plant cell wall result more points of symmetries contrast with the extremely disintegrated bordering part of the exine.
2. The new methodical supplements can be useful probably later. E.g.: After the C.P.5.A.5.10. rotation the secondary points are exclusively outside the PA (= AP) axis.
3. The repetitions of the same type of rotations seem to be extremely necessary in this case. It is worth mentioning that the not perfect rotation has resulted in interesting supplementary points of symmetries and configurations.

This work was supported by the grant OTKA—2, 24/88.

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6. QUASI-CRYSTALLOID BIOPOLYMER ORGANIZATION FROM THE SCLEREIDS OF ARMENIACA VULGARIS LAM.

Short communication

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It was emphasized previously (KEDVES, 1989), that our research program of biopolymer organization of biological objects includes all kinds of plant cell wall. Till now the sporopollenin type biopolymer structures were the subjects of our investigations, but we have several TEM data about the partially degraded plant cell wall of parenchym, xylem, and fiber (fibrous elements). TEM study of partially degraded sclereids of *Armeniaca vulgaris* LAM. were not successful for the first attempt. Reconstructed researches are in progress in this subject. Of the large program as preliminary results the following can be summarized:

1. By the light microscopical method the partially degraded sclereids seemed to be not degraded (Plate 6.1., figs. 1–3, plate 6.2., figs. 1–3).
2. The fragmentation method resulted new and interesting data.
2.1. A regular basic pentagonal polygon in Å dimension was observed (Plate 6.1., fig. 4).
2.2. Highly organized globular units of 60–110 Å in diameter were found. These units are arranged into further highly organized levels:
— filamentosus (Plate 6.1., fig. 4)
— larger globular of 220–320 Å in diameter (Plate 6.2., figs. 4, 5)
— single, compound and open polygon sensu SOUTHWORTH (1986) (Plate 6.1., fig. 4).
3. Light globular units in all probability as stabilizing elements of the metastable quasi-crystalloid skeleton were also observed (Plate 6.1., figs. 5, 6). Globular units of 4–6 Å in diameter are aligned and diversified, moreover spherical torsion of this biopolymer structure was also found. This is also an argument of the extra-quasi-crystalloid skeleton organization of this unit.

This work was supported by the grant OTKA–2, 24/88.

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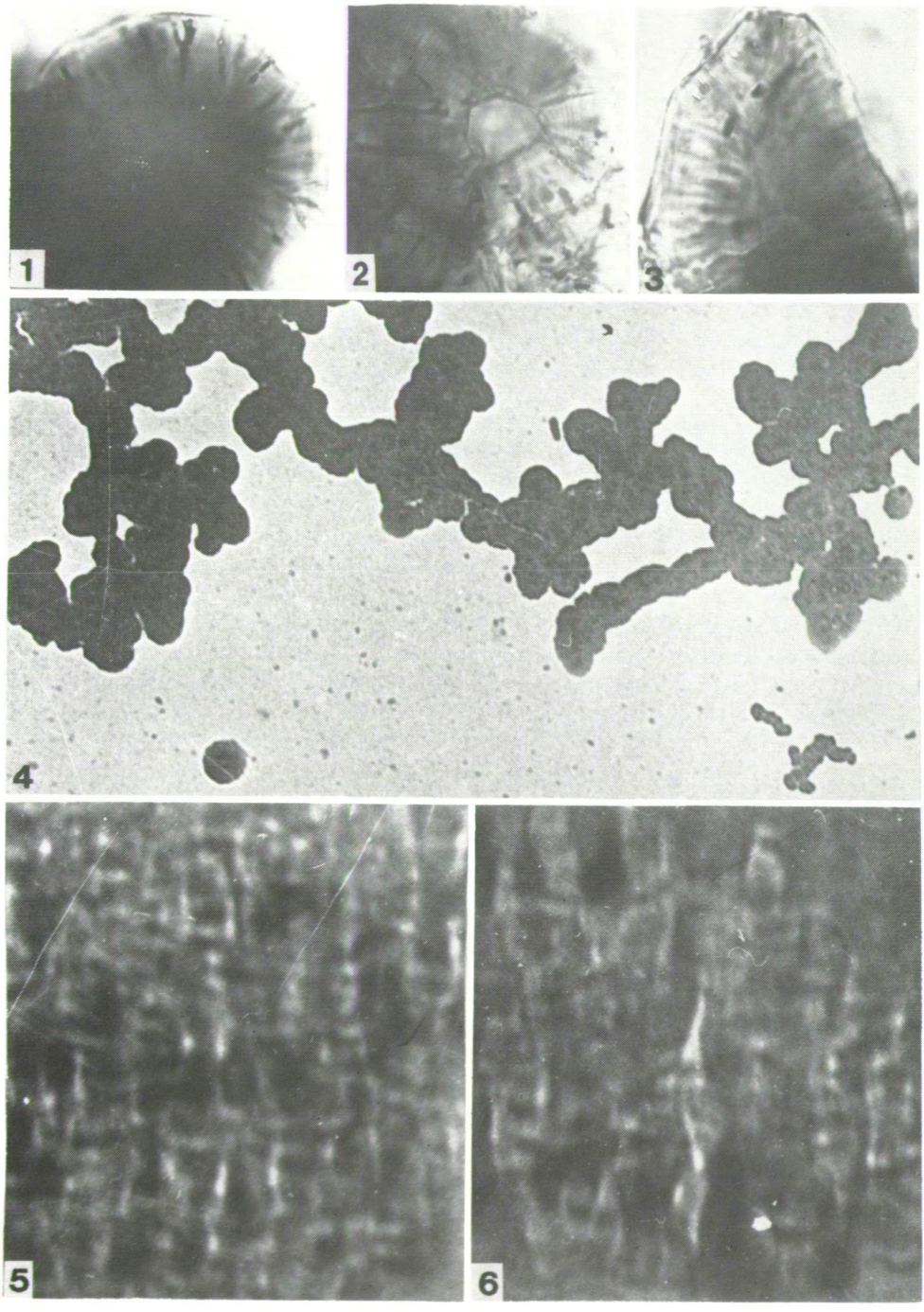
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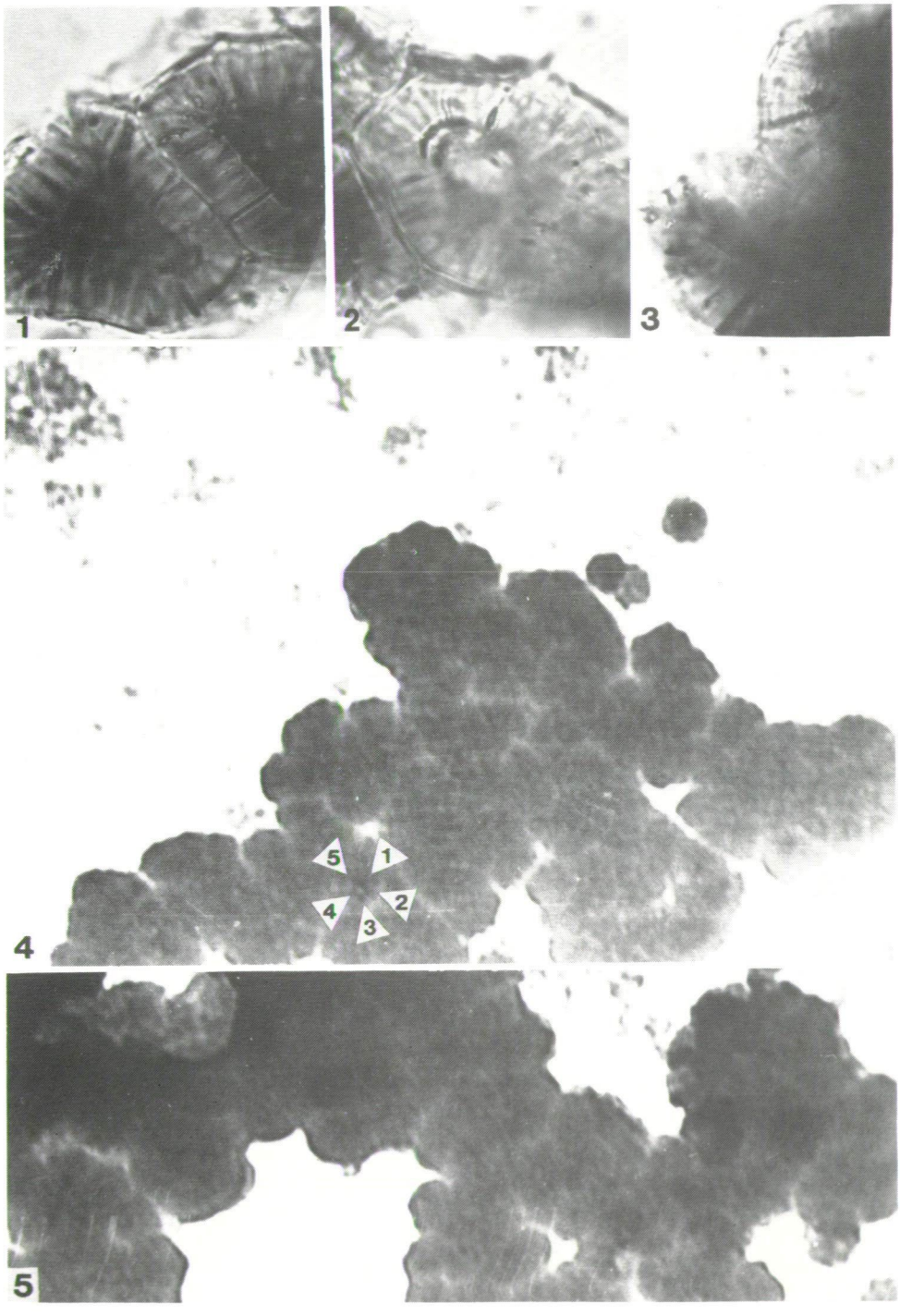
◀ Plate 6.1.

Armeniaca vulgaris LAM. sclereids
1—3. Light-microscope photographs of the sclereids after experiment No 960. 1000 x.
4. TEM picture of the biopolymer units. Experiment No 959, basic negative no 655. 50 000 x.
5,6. TEM pictures of the biopolymer structure. Experiment No 959, basic negative no 660. 500 000 x.

Plate 6.2. ▶

Armeniaca vulgaris LAM. sclereids
1—3. Light-microscope photographs of the sclereids after experiment No 964. 1000 x.
4, 5. TEM pictures of the biopolymer structure. The basic biopolymer pentagons and the highly organized globular structures are illustrated. Experiment No 963, basic negative no 670. 100 000 x.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7. THREE DIMENSIONAL MODELLING OF THE BIOPOLYMER STRUCTURE OF THE PLANT CELL WALL I.

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Motto: This is not the end. It is not even the beginning of the end. But it is perhaps, the end of the beginning.
(Sir Winston CHURCHILL, 1942)

Abstract

The three dimensional modelling of the biopolymer structure of the plant cell wall starts with this paper. The basic biopolymer unit was prepared from cardboard in a dodecahedron space arrangement. This is the basic element of the PENROSE-like biopolymer structure. One single basic element is suitable to interpret several methodical problems, such as the modified MARKHAM rotation method, and the further symmetry operations. But the quasi-crystalloid skeleton of the highly organized biopolymer structures can also be built from this basic dodecahedron skeleton. Larger PENROSE units, and a single helical structure were prepared as the first step and presented in this paper.
Key words: Plant cell, biopolymer organization, three dimensional modelling.

Introduction

It is a long time ago when the researches of the fine structure and the chemistry of the plant cell wall began. As regards the sporomorphs, a very characteristic survey was published by HESSE (1985), p. 93: "some recent observations suggest that exines are not uniform but are composed of units and subunits (ROWLEY 1981, ROWLEY et al. 1981a,b, ROWLEY and DAHL 1982). ROWLEY et al. (1981a) have used the term tuft for the exinous unit, based on glycocalyx tufts. These (helical) tuft units have an average diameter of less than 40 nm during the early stages of exine development and increase up to 100 nm, presumably by the addition of sporopollenin, during the later stages." In a previous paper (KEDVES 1989) it was emphasized that on the basis of our up-to-date knowledge four organization levels are to be distinguished:

1. Molecular structures, which can be investigated with methods of laboratory chemistry.
2. The basic biopolymer units, e.g.: the regular pentagonal polygons in angstroem dimension. These structures can be observed on the ultrathin sections or fragments

of the partially degraded plant cell walls. Symmetry and further organization can be investigated with the modified MARKHAM rotation method.
3. The so-called sub-units of the sporoderm, helical, globular units, irregular polygons, etc., in nanometer dimension.
4. Finally the higher structures of homogeneous wall substance, which can be investigated with the usual TEM method.

A three dimensional model in nanometer dimension was first published by ROWLEY et al. (1981a,b) this is the famous wire model of the helical structure. Further important establishments were published by ABADIE et. al. (1986—87). From this paper the following may be pointed out; p. 3: "For the exine types studied, a glycocalyx is differentiated by the plasma membrane (1) (glycolemma = plasma membrane and its glycocalyx) in sporal periplasm at an early tetrad stage. The nature of the glycocalyx is visualized as a fine microfilamentous structure having a helicoidal macromolecular arrangement and glycoproteinic and glycolipidic composition." "...two fundamental concepts which are:
1. the tubular skeleton of exine and
2. the relationships between the glycolemma and cytoskeleton..."

Three dimensional modelisation in nm dimension of the exine, model of a tubular subunit, and models of unit structure of the exine were published. A synthetic two dimensional scheme was published by the writer (KEDVES 1989). An attempt to the three dimensional or better say structural modelling in angstroem dimensional elements was published by GÉVAY and KEDVES (1989).

It seems to be important to emphasize that there are essential differences in consequence of the dimension of the elements of the plant cell wall: in angstroem respectively in nanometer dimension. Till this time the limit between these two province is about 20—25 Å. The quasi-crystalloid biopolymer structure is composed of pentagons of diameter below of the above mentioned "limit values". Secondary biopolymer points after rotation appeared only in angstroem dimension, and never in the so-called nm province.

Some selected non-biological basic establishments on the three dimensional modelling of the quasi-crystalloid skeleton

SACHDEV and NELSON (1985) on page 4602, Fig. 6c represents the fivefold axes of an icosahedron. This pattern corresponds to our C.P.5.A.5.10. points of symmetries. The work of HEILBRONNER (1986) is extremely important from the point of view of the symmetry in Chemistry. HARTMANN (1988); p. 467: "in stable equilibrum the symmetry elements of freely interacting systems coincide with each other as far as possible, can be regarded as one phrasing of the CURIE principle." Very important in our respect are the establishments of SCHNEER (1988), p. 395, fig. 4/a/"An icosahedron of 12 equal spheres. The radius ratio of the enclosing sphere to the largest sphere which may fit at the core is f (f is the FIBONACCI ratio 1.6180...)." MCHENRY et al. (1988) published as follows; p. 4257: "Rapidly quenched $Al_{74}Mn_{20}Si_6$ alloys are found to be either of the icosahedral structure or of the β-AlMnSi phase or a combination of these two." MADDOX's (1989) paper is also

fundamental concerning the stability of the quasi-crystalline systems, which is the large entropy. From the submitted paper of JARIC and NELSON the following may be pointed out; p. 9: "A quasiperiodic crystal is a crystal whose three dimensional FOURIER transform (or diffraction pattern) vanishes except on a discrete, but dense set of wavevectors generated by a finite set of basis vectors. This set can be called reciprocal quasilattice."

Finally some interesting statements: JEAN (1989), p. 258: "In the plant kingdom, a and m are generally two consecutive terms of the FIBONACCI series..", p. 259: "Then one comes to realize that other fields of research (e.g. the study of micro-organisms, proteins (1985), medusae and even quasi-crystals) show the same kind of symmetries." KOPTSIK and PETUKHOV (1989), p. 273: "V. I. VERNARSKY suggested that to the drastic difference between living and non-living matter there correspond the non-EUCLIDEAN space or to be more precise the space-time of the living matter."

Highly organized biological structures of the plant cell

GLOBULAR ELEMENTS

Cf. KEDVES et al. (1974) and HESSE (1985, 1986) for the fossil respectively recent exines.

FILAMENTS

KOBAYASHI et al. (1987), p. 69: "...filaments are essential components of the cytoskeleton." "We have been able to demonstrate, for the first time, a dynamic change in the arrangement of actin filaments during the differentiation of tracheary elements, and we have also found an orderly array of foci for the organization of actin filaments." P. 71: "The organization of actin filaments changes dynamically with the progression of the differentiation of tracheary elements. It should be emphasized that the disposition of the actin filaments presages the location and orientation of the secondary wall bands. It appears that actin filaments play an important role in the spatial control of deposition of the cell walls in developing tracheary elements."

HESLOP-HARRISON and HESLOP-HARRISON (1982), p. 831: "The microfibrillar polysaccharide component of the pollen intine can be isolated by progressive chemical digestion of the exine and the cellular contents and the extraction of the matrix material."

KOBAYASHI et al. (1988), p. 29: "Before thickening of the secondary wall began to occur, the actin filaments and microtubules were oriented paralell to the long axis of the cell. Reticulate bundles of microtubules and aggregates of actin filaments emerged beneath the plasma membrane almost simultaneously, immediately before the start of the deposition of the secondary wall."

Following the paper of BEVERIDGE (1988) I would like emphasize the following establishments. P. 363: "a mitochondrion is responsible for aerobic respiration...",

p. 367: "The electron-dense granules which cover the inner and outer surfaces of the wall are polycationic ferritin particles which are adhering to electronegative sites of the wall". Usually walls carry an overall net electronegative charge (Fig. 8), which makes them reactive against electropositive counter ions such as metallic cations (BEVERIDGE 1981), p. 368: "...it is reasonable to suspect that the seiving threshold would be limited to only those molecules which could fit through the polymeric interspaces." P. 369: "*Escherischia coli* walls, for example, consists of a phospholipid-lipopolysaccharide-protein bilayer..."
ROWLEY (1990) as "fundamental" structure of the exine pointed out the following. P. 25:
(1) A network of filaments is a common remnant of partly degraded exines.
(2) Spaces about 40 nm wide are usual in this "fundamental" 3—D network.
(3) Variable amounts of structure remain in these spaces (greatest perhaps in Fig. 3).
(4) Microchannels 20—25 nm wide can be tunneled out to more than twice their original diameter."

MICROTUBULES AND HELICAL STRUCTURES

HESLOP-HARRISON (1975), p. 278: "Microtubules are present at the plasmalemma during intine growth, but generally only in small numbers..." P. 282: "The lipidic fraction are accompanied by tapetal proteins and glycoproteins, which are indeed usually sealed in by the lipidic overlay." BAKHUZIEN et al. (1985); P. 43: "The microtubule distribution during the transition from interphase to the mitotic phase was examined at ultrastructural level in large highly vacuolated cells of *Nautilocalyx lynchii* and in small non-vacuolated cells of *Pisum sativum*. Both cell types contain, besides preprophase bands and perinuclear microtubules, also microtubules radiating from the nucleus into the transvacuolar cytoplasmatic strands and cytoplasm respectively." CYR et al. (1987), p. 365: "The number of cortical microtubules (MTs) increases considerably as cultured carrot (*Daucus carota* L.) cells initiate and progress through somatic embryogenesis." ROWLEY (1986—1988) pointed out as follows. P. 29: "The substructure within the endexine consists of units arranged as short tufts; these are connected to either side of white line-centered lamellations. White lines are junction planes between groups of tufts units..." Extremely intersecting are the following. P. 32: "The function of the endexine can be expected to include recognition, uptake, and other aspects of communication between a heterotrophic organism and its immediate nutritive source, the tapetum." P. 35: "My suggestion is that the channels in a bulged region work like a peristaltic pump." "I suggest that we explore a peristaltic pump-like transport role for endexines."

Following ADLER (1989), p. 17: "A phyllotactic pattern is like a living crystal." "...a helix known as the genetic spiral."
ROWLEY and DUNBAR (1990) published three dimensional diagrammatic models of the exine substructure. Five substructures (the core zone) encircled by a binding substructure.

SOUTHWORTH (1986a), p. 983: "Three types of unstained openings were associated with the granules: (i) single polygons with inner diameter up to 10 nm. (ii) compound polygons with both concave and convex sides and diameters from 15 to 25 nm and irregularly larger; and (iii) open polygons similar to either single or compound polygons in size but with one side missing." Later (SOUTHWORTH, 1986b) she wrote the following, p. 67: "Although the micrographs here show some circular profiles, several considerations argue against a helical model..."

Finally some important establishments:

HESLOP-HARRISON (1978) published a schema to the possible routes of chemical communication between walled cells. RISUENO et al. (1969) reports the first results of their investigations of the first beginnings of sporopollenin granules in the cells of the tapetum. They established as follows. P. 361: "The endoplasmatic reticulum was observed to be the system responsible for their production."
TAYLOR and TAYLOR (1987) proposed a model for the basic subunit construction of the Cretaceous megaspore wall of the genus *Selaginella* from Argentina.

Taking into consideration the previously mentioned and cited statements for the first modelling I have chosen as follows.

1. The basic PENROSE-like biopolymer unit,
2. the first and second steps of a highly organized PENROSE-like biopolymer system,
3. the basic helical or microtubular element.

Firstly the skeleton was modelled and interpreted. Further modelling is in progress, including the stabilizing biopolymer systems.

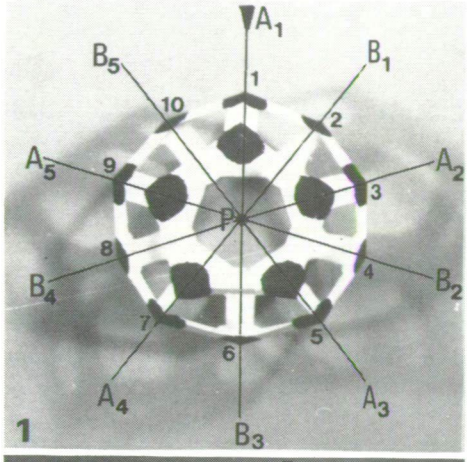
Results

The basic model of the dodecahedrane (PENROSE-like) biopolymer unit was prepared from cardboard in such a manner. The size follows the relation of the first observed regular pentagonal polygon unit on the partially degraded exine of *Pinus griffithii* MCCLELL (about 14 Å; the diameter of the model-unit is 7 cm.). The whole diameter of the basic PENROSE-like model indicates 20—25 Å, which corresponds approximatively to the measured values on the TEM pictures of the recent and fossil partially degraded exines, e.g.: KEDVES et al. (1974).

1. THE BASIC PENROSE-LIKE BIOPOLYMER UNIT
(Plate 7.1., fig. 1,2)

The investigation from different angles of this basic dodecahedron biopolymer model results extremely interesting configurations regarding the points of symmetries. At right angles to one plane which has a form of pentagonal polygon, all kinds of basic rotation points of symmetry and axes can be observed (Plate 7.1., fig. 1):

C.P.5.A.5.5.
C.P.5.B.5.5.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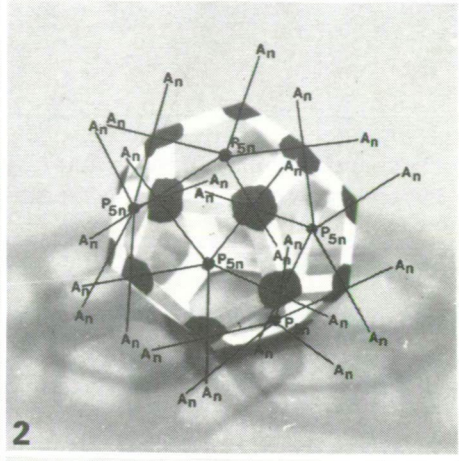
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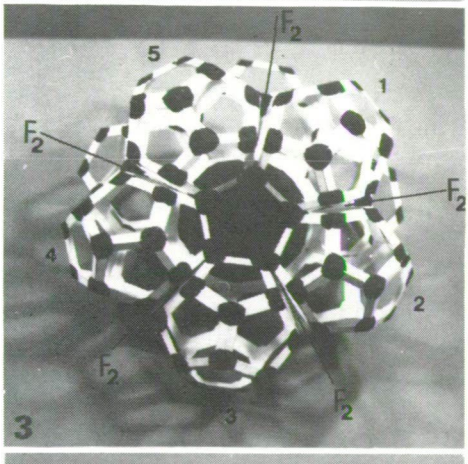
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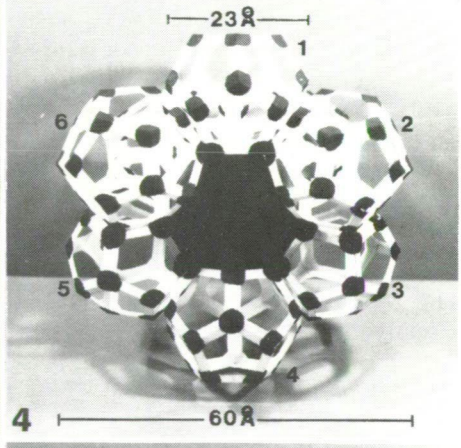
23 Å
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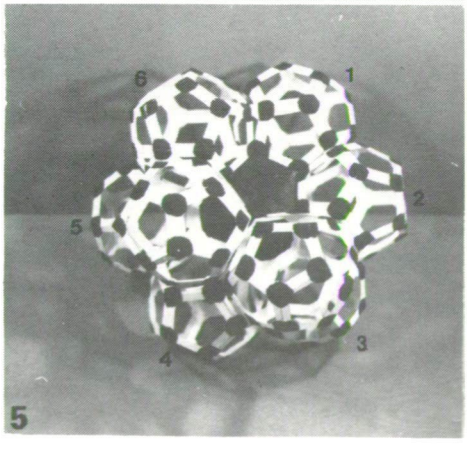
4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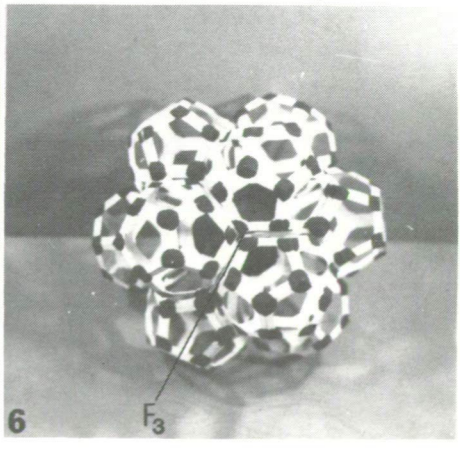

F3
6

◀ Plate 7.1.

1, 2. The model of the basic pentagon dodecahedron biopolymer unit.
Fig. 1 represents this unit in front, with the rotation axes of the modified MARKHAM rotation.
Fig. 2 is a lateral view picture of this unit with several rotation axes.
3, 6. The first step of the highly organized PENROSE-like biopolymer skeleton. This is approximatively the model of a larger globular unit.
Figs. 3—5 illustrate the not competely closed biopolymer model from different views.
Fig. 6, the complete or closed biopolymer skeleton. F_2 = frustration, the distance between two globular biopolymer elements at the edges of the pentagonal side.

C.P.5.A.5.10.
C.P.5.B.5.10.

It is interesting that the scanning electron micrograph of young flower of *Aquilegia vulgaris (Ranunculaceae)* published by ENDRESS (1987) is extremely similar to our basic three dimensional biopolymer unit.

In the case of an oblique-angled view of this unit, when approximatively three planes of the dodecahedron unit may be seen, several P values may be indicated with five AP axes by each plane (Plate 7.1., fig. 2).

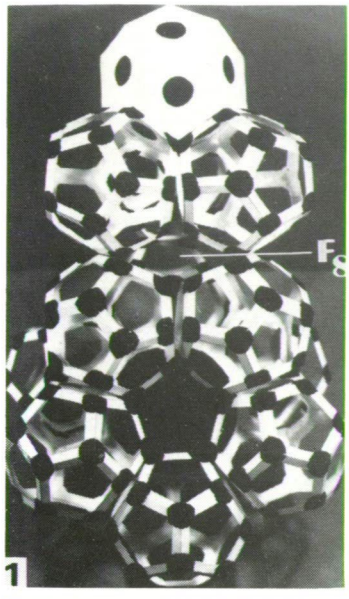
2. HIGHLY ORGANIZED PENROSE-LIKE BIOPOLYMER SKELETONS (Plate 7.1., fig. 3—6)

2.1. The first step of this modelling is when one so-called central dodecahedron biopolymer unit is surrounded with twelve same dodecahedron biopolymer units. We have prepared this kind of model as follows. The model of the "central unit" is a black and compact pentagon dodecahedron. The "building" was made as follows.

In fig. 3 of Plate 7.1. it is well shown that one plane of the "central" pentagon dodecahedron is not connected with its "corresponding" pentagon dodecahedron. The regular pentagon in the centrum and the five surrounding basic PENROSE-like units are well illustrated. The frustrations (sensu NELSON 1986) between the two edges (there are two globular biopolymer units also well illustrated, and indicated with F_2. F = frustration, the index indicates the numbers of the globular biopolymer units.) The values of the F_2 frustrations based on the measurements of these model indicate the following in angstroem dimension, for the "biological polymers": 2.2—3.0 Å.

The opposite face (Plate 7.1., fig. 4) of the above discussed plane is an apex bordered with three pentagons. The number of the surrounding dodecahedron biopolymer is six. In this way, sexangular, globular biopolymer arrangement may also appear. In fig. 4 (Plate 7.1.), the approximative sizes (diameters) in Å are also indicated. It is also necessary to point out, that the diameter of the biopolymer skeleton composed from 13 basic pentagon dodecahedron in 6 nm only. It seems to be important to emphasize this fact for the comparison of the published data in literature. We have observed several times that the same morphological unit may appear in different dimensions with different functional, phylogenetical importance.

Fig. 5 of Plate 7.1., is a semi-lateral view of the position illustrated in fig. 3, Plate 7.1.


F_8
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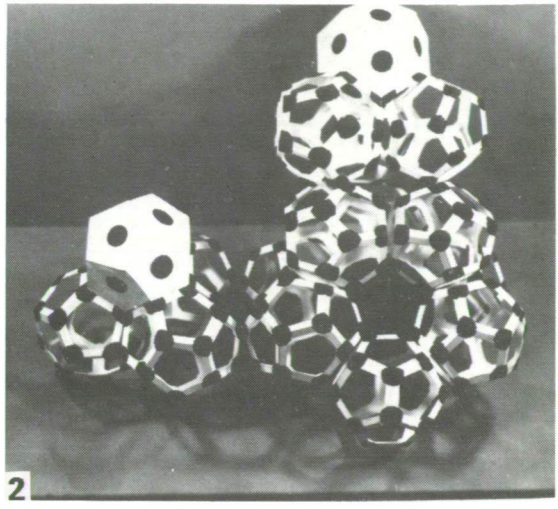
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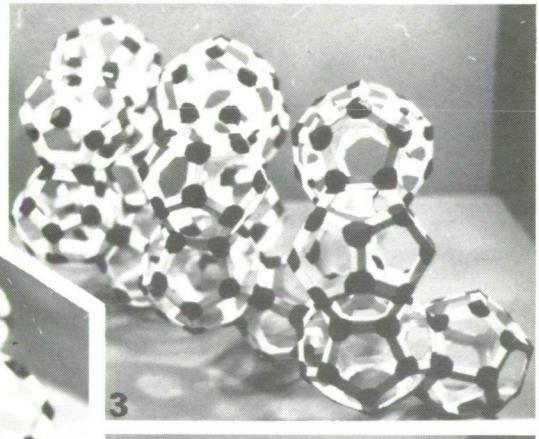
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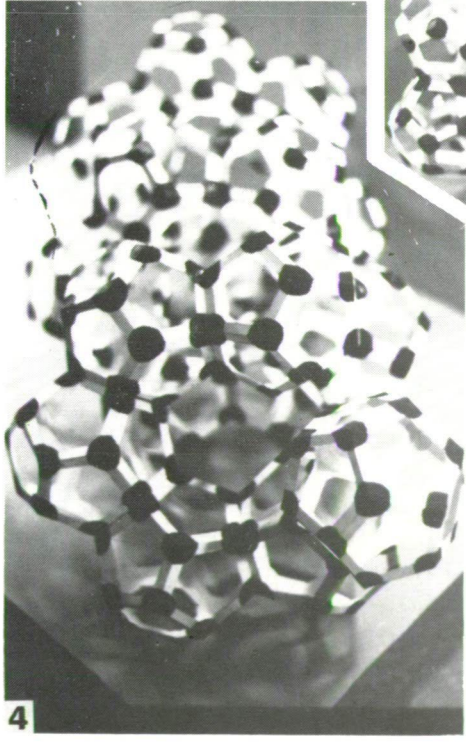
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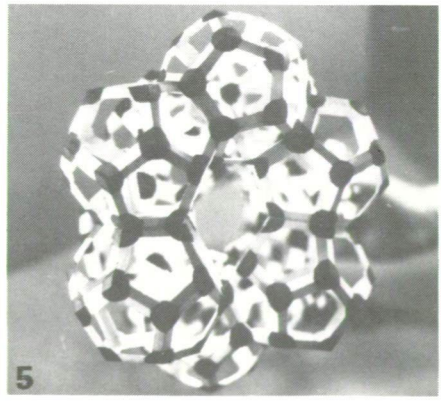
5

◀ Plate 7.2.

1, 2. First steps of the modelling of the second stage of the highly organized globular (PENROSE-like) biopolymer skeleton. The frustrations between 8 biopolymer units are extremely characteristic.
3, 5. Quasi-crystalloid biopolymer skeleton of the singlest helical (or microtubular) organization. Fig. 5 represents well the narrow central channel inside the helix.

Fig. 6, Plate 7.1. represents the completed biopolymer system of the apical view. F_3 frustration is well shown; the space between three apical globular biopolymer units. The measured values indicate 1.4—2.6 in angstroem dimension for the "biological biopolymer" unit.

2.2. To continue this kind of quasi-crystalloid biopolymer skeleton, additional elements were built (Plate 7.2., fig. 1, 2). To distinguish the central dodecahedron unit, the sides are white, with one point in the centrum. Fig. 1, of Plate 7.2., represents well the connection between two connecting sides, F_8 is relatively large. Fig. 2 of Plate 7.2., represents further connecting units. This kind of quasi-crystalloid biopolymer skeleton needs further modelling investigations.

3. HELICAL (MICROTUBULAR) QUASI-CRYSTALLOID SKELETON (Plate 7.2., figs. 3—5, plate 7.3., figs. 1—5)

The first problem to solve in this respect, is whether the basic dodecahedron model unit is suitable to be a "building" element of the helical biopolymer system? As the first step, the most single form was built and photographed from different views. These pictures represents well that from the point of view of the methods of the modified MARKHAM rotation there are a lot of opportunities. There seems in the up-to-date stage of our knowledge no reason to start the investigation of the symmetry axes of these pentagon planes. Their number is so high, but in all probability this question will be emerged secondly later with supplementary documents. Taking into consideration the size of our model this helical unit corresponds to one helical unit of the "tuft unit of the exine" published by ROWLEY, e.g. in 1981. The building of the biopolymer skeleton of the complete "wire-wound model" of ROWLEY seems to be possible but seems to be a hard job.

Discussion and conclusions

1. The first modelling of the highly organized quasi-crystalloid biopolymer skeleton justified that the basic pentagon dodecahedron biopolymer unit is really an elementary biological unit. Not only globular, but helical/tubular system was modelled in this way.

2. As it was pointed out in the published data of the different research fields in the literature, the helical/microtubular structures are extremely important in the cell biological systems. But the fibrillar and lamellar structures, in particular on the surfaces are also extremely important in cell biology. Modelling of these biopolymer structures is also in progress.

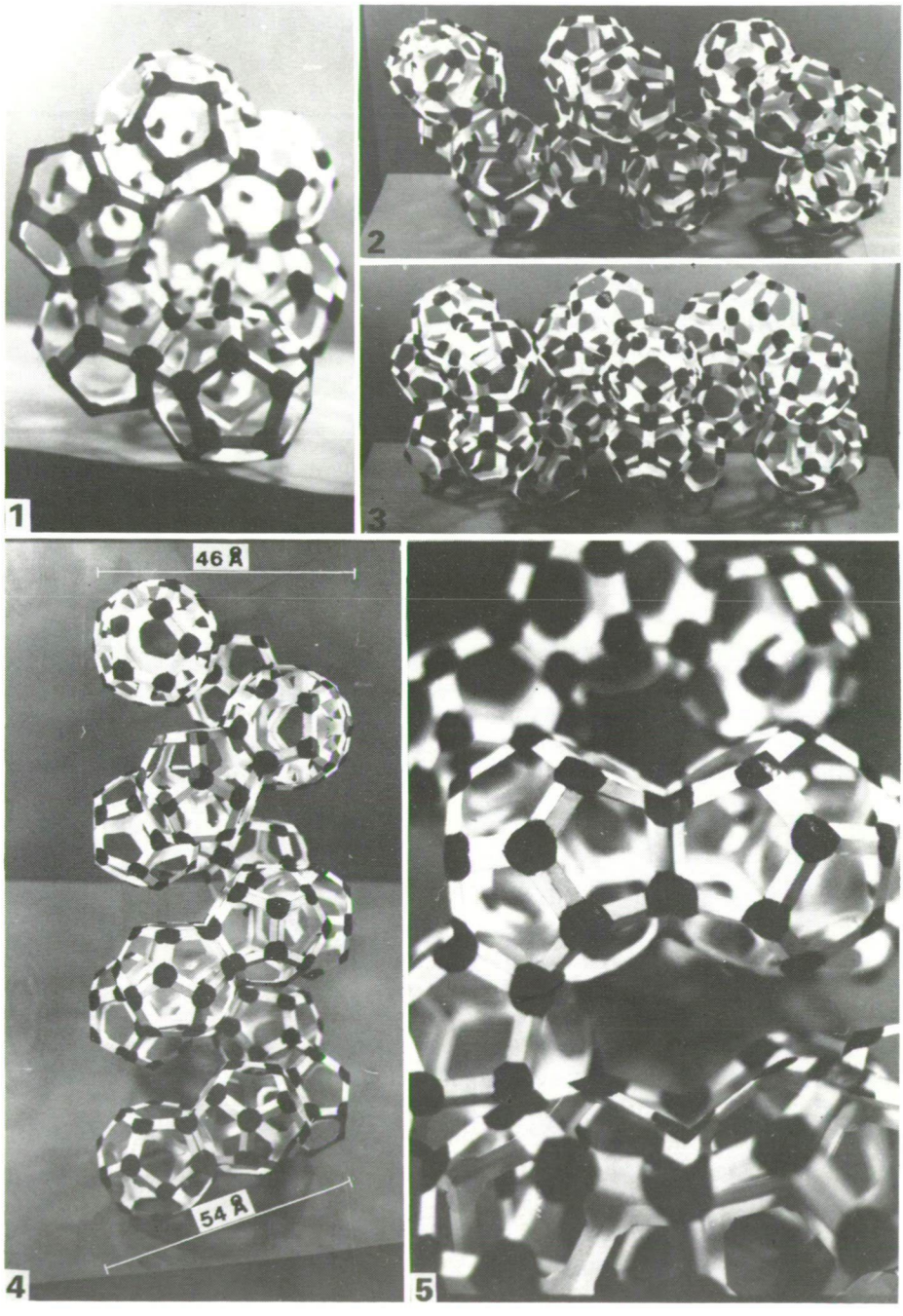

Plate 7.3.

1—5. Different views and enlargements of the helical biopolymer model.

3. Paralell to the modelling of the highly organized quasi-crystalloid biopolymer skeleton we started the modelling of the stabilizing biopolymer systems, too. As it was established in several papers, combined biopolymer structures are present in the holes of the biopolymer skeleton. These biopolymer structures have among other a stabilizing function.

4. In the future the biopolymer model of all important cell organells will be prepared.

5. Finally on the basis of our up-to-date knowledge it seems that at the biopolymer systems in nanometer dimension the rules of the PENROSE tiling are valid. In angstroem dimension, the PENROSE-model (= quasi-crystalloid) structures are present with completely different characteristic features, including biological and/or energetical characteristic features too.

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